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A STUDY OF PHYSIOLOGICAL BALANCE IN NUTRIENT MEDIA

JOHN W. SHIVE

Dissertation submitted to the Board of University Studies of the Johns Hopkins University in conformity with the requirements for the degree of Doctor of Philosophy

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JOHN W. SHIVE

ABSTRACT[2]

This publication presents the results of an experimental study of the growth of young winter wheat plants in water cultures, with respect to physiological balance of the salts in the medium and to the total concentration of the latter. Three different total concentrations were employed, of 0.1, 1.75, and 4.00 atmospheres, in terms of possible osmotic pressure. For each of these three total concentrations 36 different proportions of the three component nutrient salts, $Ca(NO_3)_2$, $MgSO_4$, and KH_2PO_4, were simultaneously tested. All possible sets of proportions of these three salts were thus included, for increments of change equal to one-tenth of the total possible osmotic pressure or diffusion tension. A small amount of ferric phosphate was added to each culture solution, to supply iron. There were 36 cultures of 6 plants each, in each concentration series and all three of these series were carried out simultaneously, and then repeated. The culture vessels held 250 cc. and the solutions were renewed every three days, for the total growth period of 23 days which was the same for both triple series. The plants were measured by five quantitative criteria and by two more qualitative ones. The quantitative criteria were: (1) dry yield of tops, (2) dry yield of roots, (3) total water loss by transpiration and guttation during the growth period, (4) water requirement per gram of dry tops, and (5) water requirement per gram of roots. The two more qualitative criteria were: (1) apparent condition of tops, especially as to two forms of leaf injury, and (2) apparent condition of roots, especially as to lateral branching.

The main results of these tests follow.

1. For young wheat plants within the first four weeks of their growth, the three salts here employed form a nutrient medium well suited to the development of the plants, when the total osmotic concentration is about 1.75 atmospheres and when the salts are present in either one of two somewhat similar sets of proportions. One of these two good solutions contains the salts in the proportions: KH_2PO_4, 0.0180 m; $Ca(NO_3)_2$, 0.0052 m; and $MgSO_4$, 0.0150 m. The other has the proportions: KH_2PO_4, 0.0108 m; $Ca(NO_3)_2$, 0.0078 m; and $MgSO_4$, 0.0020 m. In both cases about 0.0044 gram of ferric phosphate is added per liter of solution. These solutions

[1] Botanical contribution from the Johns Hopkins University, No. 46.

[2] The manuscript of this paper was received July 1, 1915. This abstract was preprinted, without change, from these types and was issued as Physiological Researches Preliminary Abstracts, vol. 1, no. 7, October, 1915.

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appear to be nearly equal physiologically; but the first is probably a little better than the second for these plants. The second produced a yield of tops 2 per cent less than the yield given by the first, and a yield of roots 1 per cent less.

2. Judging from the yields of tops and of roots, these solutions are equal to any and are superior to most of the nutrient media previously described by other investigators and now in general use for water culture work, at least when these media are prepared with a total concentration of 1.75 atmospheres.

3. For any given total concentration the best physiological balance of salt proportions for tops is not the same as that for roots.

4. For any given total concentration one set of salt proportions may be found which produces a higher yield of wheat tops than does any other set, and the same is true regarding root yields, but these two sets of salt proportions are different.

5. For any given set of salt proportions the total concentration of the medium determines the growth of the plants. It is quite impossible to select any single set of salt proportions which always produces either very low or very high relative yields throughout the three total concentrations here employed. The relative physiological value of any given set of salt proportions unquestionably varies, in general, with the total concentration of the medium, but no general rule can yet be formulated to express the manner of this variation.

6. The actual values of the top yields, for each set of salt proportions, vary with the total concentrations here employed, but not in the same order; the optimal concentration (1.75 atm.) always gives the highest yield, the supra-optimal (4.00 atm.) gives the medium yield, and the sub-optimal (0.01 atm.) gives the lowest yield.

7. The values of the cation atomic ratios $\frac{Mg}{Ca}$, $\frac{Mg}{K}$, and $\frac{Ca}{K}$ appear to determine the growth of the plants in many cases, but this relation is not always clear for any single ratio; it generally requires two of these ratio values to determine the physiological properties of the nutrient solutions with any given total concentration. The cation atomic proportions characterizing the best physiological balance, as here brought out, vary markedly, and in no simple manner, with the total concentration of the solution.

8. For total concentrations of 1.75 and 4.0 atmospheres serious disturbance of physiological balance manifests itself in more or less pronounced injury to the leaves, the conditions determining this injury being apparently related to the relative proportions of the three salts rather than to the osmotic partial concentration of any one salt.

9. Characteristic pathological conditions in the roots are also observed in those cultures where leaf injury is severe.

10. With total concentrations of 1.75 and 4.00 atmospheres the highest yields of tops were produced by cultures showing slight leaf injury and these same plants usually produced apparently more vigorous root systems than any others of their respective series, but this apparent correlation does not hold, either directly or inversely, for dry yields of roots.

11. The amount of water lost by the plants during the period of their growth appears, in a general way, to give a valuable indication of the top yields, low transpiration generally corresponding to low yields of tops and high transpiration to high yields. This generalization is especially true for the optimal and supra-optimal total concentrations of the medium (1.75 and 4.00 atm.).

12. While no general relation is manifest between the actual amounts of transpiration and the sub-optimal and optimal total concentrations, the culture of the supra-optimal series all agree in giving lower transpiration values than are given by any of the cultures of either the sub-optimal or optimal series.

13. For each set of salt proportions, the water requirement per gram of dry tops varies with the total concentration of the medium, in the reverse order; the water requirement for tops is highest for the sub-optimal concentration and lowest for the supra-optimal.

14. There appears to be no clear general relation between water requirement per gram of roots and total concentration, for the sub-optimal or optimal total concentrations. For almost every set of salt proportions this water requirement is markedly lower, however, for the supra-optimal total concentration than for either the optimal or sub-optimal.

INTRODUCTION

A culture solution may influence a plant growing in it in two ways, corresponding to the two entirely different sets of properties possessed by solutions in general. The chemical properties of the solution may affect the plant in one way, the physical properties in a very different way, and both sets of properties may have an active influence upon the growth of the plant at the same time. Perhaps the physical property of a culture solution most apt to influence plant growth is its osmotic concentration, or diffusion tension, by virtue of which it may tend to resist water absorption by plant roots.

The chemical properties of complex nutrient solutions vary widely according to the nature and proportions of the solutes present. On the other hand, the osmotic properties of a solution containing a given set of solutes in given proportions, in so far as these properties are known to affect plants, are dependent upon the total concentration and upon the extent to which the component solutes are ionized in the solution. The chemical properties and the physical properties may produce the same effect upon an organ-

ism, but in very different ways. For example, if the roots of a healthy seedling are plunged into a dilute solution of potassium cyanide, death results almost immediately. It is clear that this is a chemical effect, and that osmotic action can have no influence in bringing about the death of the plant; the solution is of very low osmotic concentration but the solute is highly poisonous. On the other hand, if the roots of such a seedling as that just mentioned be plunged into a molecular solution of cane sugar or glucose, death also results. Here it appears that the injurious action is primarily due to osmotic extraction of water from the roots; it is not due to the entrance of a poison into the organism. When such a non-poisonous solution is not sufficiently concentrated to bring about death through water removal, it may still retard growth and other forms of plant activity, and even bring about death, by hindering water absorption. In such a case the osmotic force resists water entrance instead of causing actual water exit. It is a fact of observation that plants grow less rapidly in more concentrated culture solutions (without toxic effects) than they do in solutions less concentrated but composed of the same salts in the same relative proportions. Changes in growth resulting from alterations in the total concentration of the surrounding medium seem to be dependent upon the ease with which water may be taken into the cells;[3] this is primarily an osmotic relation. A culture solution of high total concentration offers greater resistance to water absorption by plant roots than does a similar solution of lower concentration, and if the medium be sufficiently concentrated to overcome completely the absorbing power of the roots, death of the plant must soon follow from lack of water. Loeb[4] and others have shown that the osmotic extraction of water from an organism by the solution surrounding it may sometimes bring about the same effect as does a chemical change, but chemical and osmotic changes of the medium are not nearly always followed by similar responses.

In studying the chemical influence upon the plant, of the nutrient solution in which it is grown, it is therefore desirable to control, as far as possible, the osmotic influence of the medium as well as its chemical nature. This has been emphasized in the recent work of Tottingham.[5] To vary the chemical nature of the medium in which a plant is rooted, and infer that the resulting physiological reactions are due to the chemical changes in the surroundings, is not logically possible unless the osmotic properties of the

[3] See in this connection:

Livingston, B. E., On the nature of the stimulus which causes the change of form in polymorphic green Algae. Bot. Gaz. **30**: 289–317. 1900.

——— The rôle of diffusion and osmotic pressure in plants. Chicago, 1903. Pages 124–144.

——— Osmotic pressure and related forces as environmental factors. Plant World **16**: 165–176. 1913.

[4] Loeb, J., On the nature of the process of fertilization and the artificial production of normal larvae (Plutei) from the unfertilized egg of the sea urchin. Amer. Jour. Physiol. **3**: 135–138. 1899.

[5] Tottingham, W. E. A quantitative chemical and physiological study of nutrient solutions for plant cultures. Physiol. Res. **1**: 133–245. 1914.

solution are known not to have been seriously changed when the chemical properties were altered.

The general problem of the salt requirements of plants still offers many opportunities for constructive research, and nutrient solutions will surely have to be employed in experiments bearing on this problem, for salts and salt combinations can not be supplied to growing plants excepting in aqueous solution. It therefore follows that nutrient solutions and their effect upon plant growth must be well understood before very satisfactory advances in our knowledge of salt requirements may be expected. Now, in testing the effect of culture solutions upon plants growing in them, it is of course necessary to compare the growth-rate of these plants with that of others grown in some other solution used as a standard of comparison. The use of distilled water as such a standard is generally possible only with very short periods of growth, for plants in distilled water soon become unhealthy and eventually die. Thus while the growth of seedlings in distilled water may be logically compared with their growth in a nutrient solution for the first few days of their growth, it is clearly useless to compare the amounts of growth obtained in these two media during a period of, say, a month; plants in distilled water are frequently dead within two or three weeks and for the remainder of the observation period the dead cultures can furnish no better criterion for growth comparison than can an empty bottle. Even for short growth periods, the use of distilled water as a standard for comparisons has not remained unchallenged. That it is not suitable for such use is obvious, in the first place, because it removes salts from the plants. This phase of the matter has been dealt with by True and Bartlett[6] and by True.[7] Furthermore, as has been shown by many writers,[8] distilled water, unless prepared with exceptional care, appears always to contain small quantities of dissolved poisonous substances, and the resulting toxicity varies in a way not to be readily measured or controlled.

It thus appears that the standard medium required for studies of the salt-nutrition of ordinary plants must be a more or less complex salt solution. This has been somewhat tacitly recognized by many authors, and nutrient solutions for plant cultures have been the subject of many papers in the literature of plant physiology. The results of these studies have been so well brought together and digested in the first part of Tottingham's valuable paper on culture media that only very brief historical consideration is here needed.

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[6] True, R. H., and Bartlett, H. H. Absorption and excretion of salts by roots, as influenced by concentration and composition of culture solutions. U. S. Dept. Agric. Bur. Plant Ind. Bull. 231. 1912.

[7] True, R. H., Harmful action of distilled water, Amer. Jour. Bot. 1: 255–273. 1914.

[8] For literature in this connection, see:

Livingston, B. E., Further studies on the properties of an unproductive soil. U. S. Dept. Agric. Bur. Soils Bull. 36. 1907.

Hoyt, W. D., Some toxic and antitoxic effects in cultures of Spirogyra. Bull. Torr. Bot. Club 40: 333–360. 1913.

The first standard nutrient solution for plants was proposed by Sachs[9] in 1860. Since then a large number of different solutions have been recommended as producing good growth of various kinds of plants. Of these, the one most generally employed at the present time is perhaps that of Knop.[10] The medium now generally known as Knop's solution contains by weight four parts of calcium nitrate and one part each of potassium nitrate, magnesium sulphate, and either mono- or di-potassium phosphate.[11] A trace of iron is added.

Tottingham has demonstrated that Knop's solution may be markedly improved for the growth of young wheat plants by altering the proportions of the four main component salts, and it seems probable, or at least possible, that many or all the standard nutrient solutions thus far proposed might be greatly improved by similar modifications. The modified Knop's solution devised by Tottingham gives a considerably greater growth of wheat seedlings than does Knop's solution itself. Certainly, the plan adopted by Tottingham in working out the salt proportions of his nutrient solution, is the most logical and complete method which has appeared in the literature up to the present time, and the solution which he recommends for young wheat plants, based upon such thoroughgoing experimentation as it is, must be regarded as the nearest approach to a standard nutrient medium so far described.

Tottingham employed eighty-four different solutions, all of approximately the same total osmotic concentration, but each solution differing from all the others in its proportions of the four main salts, mono-potassium phosphate, potassium nitrate, calcium nitrate, and magnesium sulphate. Each solution also contained the usual trace of iron, as ferric phosphate, the amount of this salt being the same in all cases. Tests of these eighty-four different sets of proportions of the main nutrient salts, with total osmotic concentrations of 2.50 atmospheres (about the optimum total concentration for young wheat plants) showed that the best solution for the growth of tops during the first four weeks after germination contained the salts in the following volume-molecular proportions: mono-potassium phosphate, 0.0130 m; potassium nitrate, 0.0049 m; calcium nitrate, 0.0144 m; magnesium sulphate, 0.0145 m. This solution showed an improvement of 11 per cent over Knop's solution of the same osmotic concentration, the percentage being calculated on the basis of dry weight of tops grown in the latter solution. The present writer has repeated the tests of Tottingham's optimal series of

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[9] Sachs, J., Vegetationsversuche mit Ausschluss des Bodens über die Nährstoffe und sonstigen Ernahrungsbedingungen von Mais, Bohnen und anderen Pflanzen. Landw. Versuchsst. **2**: 219–268. 1860.

[10] Knop, W., Quantitative-analytische Arbeiten über den Ernährungsprocess der Pflanzen. II. Landw. Versuchsst. **4**: 173–187. 1862.

[11] The di-potassium salt seems to be more frequently met with in the literature than is the mono-potassium salt, in connection with Knop's solution, but the latter is by far the more satisfactory of the two, on both chemical and physiological grounds, as has been clearly and convincingly shown by Tottingham.

eighty-four solutions as compared to Knop's solution (all of them having the same osmotic concentration, 2.50 atmospheres), with wheat, and the results are in very satisfactory agreement with those obtained by the earlier author. The best growth of tops (measured in terms of dry weight) occurred with the same proportions of salts as those giving the best growth in the earlier work. While Tottingham reports, for his best solution, an improvement of 11 per cent over Knop's proportions, the corresponding improvement in the repeated experiment was 12 per cent.

From a consideration of Tottingham's work, as well as from earlier publications, it is clear that nutrient solutions prepared according to the formulas of Knop and Tottingham are very suitable for supporting plant growth, and Tottingham's solution may safely be employed as a standard for culture comparisons. However, in all experimentation bearing on the growth of plants in nutrient solutions, and related to the general problems of salt requirements, physiological balance, and salt antagonism, it is quite essential that the standard nutrient solution used as a basis of comparison be as simple as possible, besides being capable of producing excellent growth. Whatever salts the standard solution may contain, it should be characterized by approximately optimum salt proportions and, at the same time, should have approximately optimum osmotic concentration for the particular kind of plant upon which the experimentation is to be carried out. Since it may be supposed that different plant forms may differ in their requirements for a physiologically balanced solution, it is clear that such a chemically and physically optimum solution can not be satisfactorily determined by the usual hit-or-miss procedure in such cases (calling that *optimum* which has been shown only to be *good*), but must rest upon a more or less thorough testing of a rather large number of possibilities. Tottingham's general method for finding the optimum solution for a given set of salts and for a given plant is the only one available, and, although it may appear somewhat elaborate and tedious in operation, yet its employment is quite essential if the physiological properties of the medium in which growth is to be taken as standard are to be at all well understood. It thus appears that studies on salt nutrition will frequently have to involve some such series of tests as those employed by Tottingham. In such work, the simpler the mixture may be, the more readily may its optimum, as regards salt proportions and osmotic concentration, be determined. If a simple series of salts may be so brought together as to give as good plant growth as does the optimal mixture of a more complex series, the former is much to be preferred.

The experimentation here to be set forth aimed primarily to find out whether a simpler solution than that used by Tottingham might not be possible, without loss of ability to support plant growth. Possible simplification lies here only in the employment of a smaller number of salts. Tottingham used four main salts in eighty-four different combinations for each osmotic

concentration tested. If the number of salts might be reduced to three, a similar series of tests (increments of partial concentrations being, as in Tottingham's work, one-tenth of the total concentration), would involve only thirty-six different combinations, which would entail a saving of work greatly to the advantage of rapid progress. If a two-salt solution might be employed, such a series of tests would include but nine combinations, but such a solution is clearly impossible in the present case, since six different chemical elements (K, Ca, Mg, N, S, and P) are required in every adequate nutrient medium, and only two of these can be carried by a single salt. It appears, then, that a three-salt mixture (neglecting the trace of iron, which is of course always to be added) is logically possible as a standard culture solution, and that such a standard solution containing but two salts is impossible on *a priori* grounds.

The omission of potassium nitrate from the Knop-Tottingham formula leaves the three salts, mono-potassium phosphate, calcium nitrate, and magnesium sulphate, which, with the trace of ferric phosphate also present, contain all the essential elements required in a nutrient solution. These dissociate in solution to form all the ions present in the Knop-Tottingham four-salt solution. They do not precipitate too readily when mixed in solution, and they permit total concentrations suitable for plant growth. Such a three-salt solution seems to be chemically as well adapted to the growth of plants in water culture as is the Knop-Tottingham four-salt solution.

It was the purpose of this investigation to study the properties and possibilities of the three-salt combination just suggested, and to determine, as nearly as possible, the salt proportions needed to produce approximately optimal growth of wheat and of buckwheat, during early stages of their development. The results obtained with wheat will alone be presented in the present paper; those for buckwheat will be published later.[11a]

The investigation was carried out at the Laboratory of Plant Physiology of the Johns Hopkins University. It is a pleasure to acknowledge indebtedness to Professor Burton E. Livingston, not only for suggesting the problem, but also for helpful advice during the progress of the work, and for valued aid and criticism in the preparation of the manuscript.

MATERIALS AND METHODS

THE STOCK SOLUTIONS OF SINGLE SALTS

The salts used in the present work were Merck's "highest purity" mono-potassium phosphate and calcium nitrate, and Merck's "blue label" magnesium sulphate, the last containing the usual seven molecules of water.

[11a] A preliminary report of some of the results of the present study has already appeared:—Shive, J. W., A three-salt nutrient solution for plants. Amer. Jour. Bot. 2 : 157-160. 1915.

It was found necessary to dry the calcium nitrate, because of varying amounts of water in the lumps of salt. This was accomplished by heating the salt in a large crystallizing dish in an electric oven at 150°C., until it formed a solid mass. It was then pulverized in a mortar, returned to the oven, and dried to constant weight at 150°C. Any free moisture contained in the stock supply of the other salts was eliminated by drying them at 105°C. and allowing them to cool in a desiccator, from which they were taken as needed.

In preparing the original stock solutions, from which, after further dilution, the culture solutions were to be made up, gram-molecular weights of the salts (weighed to one milligram) were dissolved separately in Jena glass flasks, and each solution was then made up to liter volume at 15°C. These solutions were always stored in the flasks in which they were prepared, but were never kept for a long time; in no case longer than six days. The distilled water used throughout was obtained from a "Barnstead" still, with tin-lined condenser, and was stored in a twenty-gallon stone-ware jar, from which it was drawn through a block tin tube into a glass carboy for immediate use. Throughout this work, special precautions were taken to clean thoroughly (with potassium bichromate in sulphuric acid followed by thorough rinsing) all vessels employed as containers of distilled water or of solutions.

For immediate use the volume-molecular single salt solutions were diluted to concentrations better suited to the preparation of the culture media themselves. These diluted stock solutions were kept in liter flasks. Each of these flasks was connected with the upper end of a 50 cc. burette, graduated to 0.1 cc. and provided with a glass stopcock below. The connection was made by means of a glass tube bent into the form of an inverted U, one end extending to the bottom of the flask, the other passing through a tightly fitting stopper in the top of the burette and extending downward just to the zero mark on the burette scale. A second glass tube was also passed through the stopper in the top of the burette, and ended just below the lower surface of this stopper. Suction applied to this tube caused the solution to flow from the flask into the burette, thus filling the latter. Since the longer arm of the U-tube extended to the bottom of the flask, and since the zero of the burette scale was always at a higher level than the surface of the liquid in the flask, any excess of solution in the burette siphoned back into the flask when suction was discontinued, leaving the burette filled to the zero mark. In this way the solutions came into contact with glass surfaces only, and this device for automatically obtaining the proper level in the burette after each measurement was found to be a valuable saver of time. The concentrations of these diluted stock solutions were so calculated that no less than 2 cc. of any one was ever drawn from the burette at one time, in the preparation of the culture solutions; errors that might result from slight inaccuracies in reading burettes graduated only to 0.1 cc. were thus largely obviated.

THE CULTURE SOLUTIONS

In a series of solutions having three given constituent salts, the relative proportions of these three salts may, of course, be varied so as to give a very large number of solutions, all of the same total concentration; and the total concentration of a culture solution with any given set of proportions of the three salts may likewise be varied to give another large number of solutions, differing neither in the kind of salts nor in their relative proportions, but only in the total concentration.

Throughout this paper, concentrations will be expressed in terms of diffusion tension or maximum osmotic pressure (osmotic concentration), in atmospheres, or in terms of gram-molecules per liter of solution (volume-molecular concentration).

Three series of nutrient solutions were employed, each solution containing the three salts, mono-potassium phosphate, calcium nitrate, and magnesium sulphate, in varying proportions. These three series differed widely in total concentration, and were so chosen that one possessed a total concentration about optimal for wheat as here grown, one of the others being below, and one above this total concentration. All solutions of the same series had approximately the same osmotic concentration. Tottingham called attention to the fact that the concentration employed for his optimal series (2.50 atmospheres of diffusion tension) may be slightly above that required for optimal growth of wheat, and the results of preliminary experiments with three-salt mixtures, in series such as are to be described below, showed that a total salt concentration of 1.75 atmospheres is well within the range required for optimal growth of wheat. These tests showed further that a concentration or 4.0 atmospheres is well above the optimal range for wheat. The following experiments were therefore carried out with three series of nutrient solutions having concentrations of 0.1, 1.75, and 4.0 atmospheres, the first being chosen as having been shown by preliminary tests to lie well below the optimal range of total concentration for the plant here employed. These three series will hereafter be termed sub-optimal (0.1 atm.), optimal (1.75 atm.), and supra-optimal (4.0 atm.).

The method here adopted to control the osmotic concentrations in a series of solutions differing in the proportions of the three salts used was the same as that employed by Tottingham. In varying the relative proportions of the component salts apportionments were made in such a way that a decrease in the partial concentration of one salt was balanced by increases in the partial concentrations of the remaining salts, sufficient to keep the total osmotic concentration of the solution constant. The total osmotic concentration to be employed for any series was considered to be divided into ten equal parts and these parts were distributed among the three salts in all possible proportions. Thus each salt produced, in the different solutions of the same series, from one to eight-tenths of the total osmotic concentration.

A detailed discussion of the methods of calculation by which the partial diffusion tension and volume-molecular concentration of each salt, for such complex mixtures with a fixed total osmotic concentration, may be approximately determined, has been presented by Tottingham (pp. 177–182 and 192) and need not be repeated here. The calculations were carried out in such a manner as to allow every three-salt solution to contain that particular amount of each salt which would have been required to produce the desired partial osmotic concentration if that salt had been alone in the solution. Each solution contained an amount of each of the three salts such that the total osmotic concentration should possess the fixed magnitude required by the particular series to which the solution belonged, if it were assumed that the presence of the remaining two salts exerted no influence upon its degree of ionization. Expressed in another way, each of the three salts may be conceived as placed in the solution of the other two as though that solution were pure water, so as to give the requisite osmotic concentration for the first salt (one, two, etc., tenths of the total diffusion tension of the complete solution) without any reference to the presence of the other two.

The lowering of the freezing-point was determined for all of the three-salt solutions here employed, and the osmotic concentration was calculated from the lowering in each case. The method here used was the same as that described by the writer in connection with his study of Tottingham's solutions.[12] From these determinations it appeared that the lowerings were approximately the same for all of the complete solutions of the sub-optimal and optimal series. It therefore follows, in these cases, from the relation holding between the lowering of the freezing-point and maximum possible osmotic pressure, that the amount of salt required to produce one-tenth of the total osmotic concentration of the complete solution was also constant for the sub-optimal and for the optimal series. This amount may be termed the osmotic unit for the series in question, following Tottingham's similar usage. In the supra-optimal series, however, the value of this osmotic unit was variable, becoming greater or less in magnitude as the partial osmotic concentration of the salt in question was increased or decreased. This, of course, is to be expected in such solutions as these, where the concentration of the salt is too high to permit approximately complete dissociation.

The volume-molecular partial concentrations of the solutions in the supra-optimal series were calculated to give a total osmotic concentration of 4.50 atmospheres, but the cryoscopic tests gave depressions of the freezing-point indicating a total osmotic concentration of only about 4.0 atmospheres in every case, throughout the entire series. This seems to indicate that the decrease in the degree of dissociation caused by the influence of one salt upon another is considerable in these more concentrated mixtures. With the

[12] Shive, J. W., The freezing points of Tottingham's nutrient solutions. Plant World **17**: 345–353. 1914. In table I, page 349, of this paper, the second number in the fifth column should be **2.53** instead of 2.40 as given.

lower concentrations, sub-optimal and optimal, this influence is lacking, or is too slight to be detected by the methods here employed. Tottingham's supra-optimal series of nutrient solutions showed a similar depression in total osmotic concentration when this was determined by the cryoscopic method (Shive [1914]). The average diffusion tension of that entire series was 7.22 atmospheres, while Tottingham's calculation placed this value at 8.15 atmospheres.

The subject of dissociation equilibrium in solutions of two salts possessing a common ion is treated in text-books of physical chemistry, but the influence of one salt upon the dissociation of others in complex solutions where no common ion is present has not yet been worked out satisfactorily. Mellor[13] points out that there is no interchange of ions in mixed solutions of strongly dissociated electrolytes, but that the solutions contain the same ions as were previously present in the unmixed solutions. With feebly dissociated electrolytes the phenomenon is much more complex, and is not yet understood well enough to allow satisfactory calculation.

The results of the cryoscopic tests justify the supposition that all the solutions of the sub-optimal series possessed a total osmotic concentration of 0.1 atmosphere, and, similarly, that those of the optimal series had a total concentration of 1.75 atmospheres, within the limits of accuracy imposed by the cryoscopic method as here employed. Since the solutions of the supra-optimal series agreed in showing a lowering of the freezing-point corresponding to a diffusion tension of 4.0 atmospheres, instead of 4.50 as calculated, it is safely to be supposed that these solutions actually exhibited an osmotic concentration very close to 4.0 atmospheres. In default of more precise knowledge, these suppositions will be regarded as true in the following discussions. Whatever may be the magnitude of the errors thus involved, it is certain that such variations from the assumed osmotic concentration can not be great enough in any case to produce any sensible influence upon the plants; such organisms are much less sensitive to osmotic conditions of the medium than is the cryoscopic method of determination as here used.

Table I gives the volume-molecular partial concentrations of each salt required to produce from one-tenth to eight-tenths of the total osmotic concentration, for each of the three series of solutions here considered. To determine the volume-molecular partial concentration of any salt in any solution of the three series, it is necessary simply to find in the first column the number indicating how many tenths of the total osmotic concentration are to be apportioned to the particular salt in question, and then to read the required partial volume-molecular concentration, given opposite this number on the same line, in the proper column for the particular series and salt involved.

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[13] Mellor, J. W., Chemical statics and dynamics. London, 1909. Pages 202–205.

For convenience in the preparation of the three series of complete nutrient solutions to be described later, the concentrations of the stock solutions from which the culture solutions were prepared differed widely in the three series, but the three separate stock solutions used in the preparation of each single series were equal in molecular concentration. The concentrations of the stock solutions used in the preparation of the sub-optimal, optimal, and supra-optimal series were one-fortieth volume-molecular (m/40), one-fourth volume-molecular (m/4), and volume-molecular (m), respectively.

In preparing a culture solution, the required amount of stock solution of mono-potassium phosphate was first drawn from the proper burette into a 250 cc. volumetric flask about three-fourths filled with water. To this was now added, in a similar manner, the required amounts of the stock solutions of calcium nitrate and of magnesium sulphate, in the order here given. As

TABLE I

Volume-molecular partial concentrations of mono-potassium phosphate, calcium nitrate, and magnesium sulphate required to produce from one to eight tenths of the total osmotic concentration, for each of the three series of solutions

TENTHS OF TOTAL CONCENTRATION	SUB-OPTIMAL SERIES (TOTAL CONCENTRATION 0.1 ATM.)			OPTIMAL SERIES (TOTAL CONCENTRATION 1.75 ATM.)			SUPRA-OPTIMAL SERIES (TOTAL CONCENTRATION 4.0 ATM.)		
	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$
1	0.0002	0.00015	0.0003	0.0036	0.0026	0.0050	0.0090	0.0066	0.0142
2	0.0004	0.00030	0.0006	0.0072	0.0052	0.0100	0.0180	0.0132	0.0258
3	0.0006	0.00045	0.0009	0.0108	0.0078	0.0150	0.0270	0.0189	0.0428
4	0.0008	0.00059	0.0011	0.0144	0.0104	0.0200	0.0368	0.0265	0.0570
5	0.0010	0.00074	0.0014	0.0180	0.0130	0.0250	0.0460	0.0331	0.0713
6	0.0012	0.00089	0.0017	0.0216	0.0156	0.0300	0.0580	0.0417	0.0890
7	0.0014	0.00104	0.0020	0.0252	0.0182	0.0350	0.0690	0.0496	0.1070
8	0.0017	0.00119	0.0023	0.0288	0.0208	0.0400	0.0800	0.0576	0.1240

the solutions were added, the flask was shaken to promote mixing. The volumetric flask was finally filled to the mark with water.

To each complete solution, as it was prepared, was added three drops of a uniform suspension of ferric phosphate in distilled water. Each cubic centimeter of this suspension contained approximately 0.0022 g. of ferric phosphate, or 0.00082 g. of iron. The ferric phosphate was prepared by precipitation from a solution of ferric nitrate with mono-potassium phosphate, and the precipitate was subsequently thoroughly washed.

Variations in the proportions of the three salts here employed, by increments of one-tenth of the total osmotic concentration, produce a series of thirty-six solutions, as has been remarked. Similar variations in the four salts used by Tottingham yield a series of eighty-four solutions. The smaller number of solutions is a distinct advantage in favor of a three-salt medium,—

an advantage that can scarcely be overestimated, considering the large number of cultures to be dealt with in studies of this kind.

For the concrete expression of the relative osmotic proportions of the three salts in each solution of each series, for facility in designating individual cultures, and for ease of reference in discussion, the thirty-six solutions may be conveniently arranged on a triangular diagram, as shown in figure 1. Graphic schemes similar to this have been used extensively in physical chemistry, for considerations involving relative proportions of three component parts. The diagram as here used was employed by Schreiner and Skinner[14] in a study somewhat similar to the present one. Each side of an equilateral triangle is divided into seven equal parts, and lines are drawn through each of the points of division thus obtained, parallel to each of the other two sides

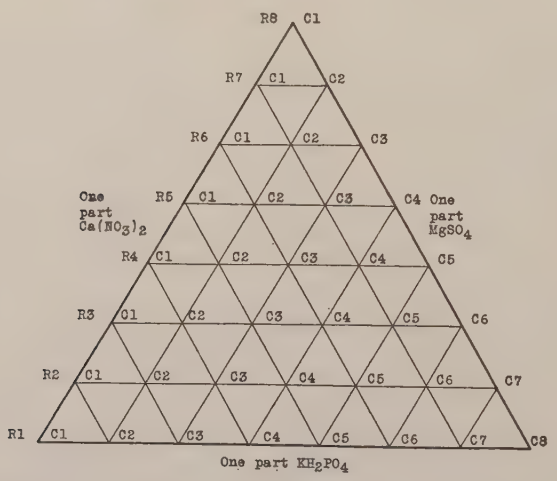
R8 C1
R7 C1 C2
R6 C1 C2 C3
One part $Ca(NO_3)_2$
R5 C1 C2 C3 C4
One part $MgSO_4$
R4 C1 C2 C3 C4 C5
R3 C1 C2 C3 C4 C5 C6
R2 C1 C2 C3 C4 C5 C6 C7
R1 C1 C2 C3 C4 C5 C6 C7 C8
One part KH_2PO_4

FIG. 1. Diagram showing solution numbers and osmotic proportions of the three salts.

of the triangle. Each of the original points and each of the intersections of the lines represents a culture solution or a culture. The diagram shows eight horizontal rows of cultures, one above the other. The lowest row contains eight cultures, the next seven, etc., and the eighth row contains but a single one. All the solutions represented in the lowest row have approximately one-tenth of their total osmotic concentration due to mono-potassium phosphate, those in the second row have approximately two-tenths due to this salt, and so on, until the apex of the triangle is reached. This culture, representing the eighth row, has approximately eight-tenths of its total

[14] Schreiner, O. and Skinner, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth, Bot. Gaz. 50: 1–30. 1910.

osmotic concentration due to mono-potassium phosphate. The first culture at the left of each row has one-tenth of its total osmotic concentration due to calcium nitrate, the second culture of each row has two-tenths derived from this salt, and so on to the opposite side of the triangle. Thus the eight cultures of the first row have, respectively, from one-tenth to eight-tenths of their total osmotic concentration due to the calcium salt. The seven cultures of the second row have from one-tenth to seven-tenths of their osmotic concentration derived from the calcium salt, and so on to the apex of the triangle. The last culture of each row has one-tenth of its total osmotic concentration derived from magnesium sulphate. Proceeding from the right to the left side of the triangle, the partial osmotic concentration of magnesium sulphate in each solution increases in a manner similar to that followed for calcium nitrate passing in the opposite direction. Thus the eight cultures of the first row have from one-tenth to eight-tenths of their osmotic concentration due to calcium nitrate, and from eight-tenths to one-tenth produced by magnesium sulphate, and in the cultures of each succeeding row, the osmotic proportions of these two salts are similarly distributed. Each side of the diagram may be designated by the name of one of the three salts; thus the base (as shown in fig. 1) may be considered as the mono-potassium side, while the left and right sides are, respectively, the calcium nitrate and the magnesium sulphate sides.

The method adopted by Tottingham (p. 194) to designate individual cultures is again employed here. The rows of cultures are numbered R1 to R8, from base to apex of the triangle, and the individual cultures are numbered in each row from left to right, C1 to C8. Thus the cultures of the first row are numbered R1C1 to R1C8, the cultures of the second row, R2C1 to R2C7, etc., until the single culture of the eighth row is numbered R8C1. To determine the osmotic proportions of the salts in any culture solution, it is only necessary to observe the row in which it occurs and its number in the row. Thus, culture R4C2 has four-tenths of its osmotic concentration due to mono-potassium phosphate, since it is in row four; two-tenths due to calcium nitrate, since it is culture number two from the left side; and four-tenths derived from magnesium sulphate, since it is the fourth culture from the right side of the triangle.

In table II are given the actual partial volume-molecular concentrations of each solution of the three series used in the present study. The solution numbers in the table correspond to the numbers in the diagram of figure 1, already explained.

It will be observed that solutions R1C3 to R1C8, also R2C4, R2C5, and R2C7, of the supra-optimal series, are omitted from this table. These solutions formed slight precipitates after standing from one to three days, and were rejected on that account, as not suitable for a study of this kind.

TABLE II

Partial volume-molecular concentrations of mono-potassium phosphate, calcium nitrate, and magnesium sulphate in the solutions employed in the sub-optimal, optimal, and supra-optimal series.

SOLUTION NUMBER	PARTIAL CONCENTRATION, VOLUME-MOLECULAR								
	Sub-optimal series (0.1 atm.)			Optimal series (1.75 atm.)			Supra-optimal series (4.00 atm.)*		
	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$
R1C1	0.00021	0.00015	0.00228	0.0036	0.0026	0.0400	0.0090	0.0066	0.1240
C2	0.00021	0.00030	0.00199	0.0036	0.0052	0.0350	0.0090	0.0132	0.1070
C3	0.00021	0.00045	0.00171	0.0036	0.0078	0.0300	.....	.....	.....
C4	0.00021	0.00059	0.00124	0.0036	0.0104	0.0250	.....	.....	.....
C5	0.00021	0.00074	0.00114	0.0036	0.0130	0.0200	.....	.....	.....
C6	0.00021	0.00089	0.00086	0.0036	0.0156	0.0150	.....	.....	.....
C7	0.00021	0.00104	0.00057	0.0036	0.0182	0.0100	.....	.....	.....
C8	0.00021	0.00119	0.00028	00.036	0.0208	0.0050	0.0090	0.0576	0.0142
R2C1	0.00041	0.00015	0.00199	0.0072	0.0026	0.0350	0.0180	0.0066	0.1070
C2	0.00041	0.00030	0.00171	0.0072	0.0052	0.0300	0.0180	0.0132	0.0890
C3	0.00041	0.00045	0.00142	0.0072	0.0078	0.0250	0.0180	0.0198	0.0713
C4	0.00041	0.00059	0.00114	0.0072	0.0104	0.0200	.....	.....	.....
C5	0.00041	0.00074	0.00086	0.0072	0.0130	0.0150	.....	.....	.....
C6	0.00041	0.00089	0.00057	0.0072	0.0156	0.0100	0.0180	0.0417	0.0285
C7	0.00041	0.00104	0.00028	0.0072	0.0182	0.0050	.....	.....	.....
R3C1	0.00062	0.00015	0.00171	0.0108	0.0026	0.0300	0.0270	0.0066	0.0890
C2	0.00062	0.00030	0.00142	0.0108	0.0052	0.0250	0.0270	0.0132	0.0713
C3	0.00062	0.00045	0.00114	0.0108	0.0078	0.0200	0.0270	0.0198	0.0570
C4	0.00062	0.00059	0.00086	0.0108	0.0104	0.0150	0.0270	0.0265	0.0428
C5	0.00062	0.00074	0.00057	0.0108	0.0130	0.0100	0.0270	0.0331	0.0285
C6	0.00062	0.00089	0.00028	0.0108	0.0156	0.0050	0.0270	0.0417	0.0142
R4C1	0.00082	0.00015	0.00142	0.0144	0.0026	0.0250	0.0368	0.0066	0.0713
C2	0.00082	0.00030	0.00114	0.0144	0.0052	0.0200	0.0368	0.0132	0.0570
C3	0.00082	0.00045	0.00086	0.0144	0,0078	0.0150	0.0368	0.0198	0.0428
C4	0.00082	0.00059	0.00057	0.0144	0.0104	0.0100	0.0368	0.0265	0.0285
C5	0.00082	0.00074	0.00028	0.0144	0.0130	0.0050	0.0368	0.0331	0.0142
R5C1	0.00103	0.00015	0.00114	0.0180	0.0026	0.0200	0.0460	0.0066	0.0570
C2	0.00103	0.00030	0.00086	0.0180	0.0052	0.0150	0.0460	0.0132	0.0428
C3	0.00103	0.00045	0.00057	0.0180	0.0078	0.0100	0.0460	0.0198	0.0285
C4	0.00103	0.00059	0.00028	0.0180	0.0104	0.0050	0.0460	0.0265	0.0142
R6C1	0.00123	0.00015	0.00086	0.0216	0.0026	0.0150	0.0580	0.0066	0.0428
C2	0.00123	0.00030	0.00057	0.0216	0.0052	0.0100	0.0580	0.0132	0.0285
C3	0.00123	0.00045	0.00028	0.0216	0.0078	0.0050	0.0580	0.0198	0.0142
R7C1	0.00144	0.00015	0.00057	0.0252	0.0026	0.0100	0.0690	0.0066	0.0285
C2	0.00144	0.00030	0.00028	0.0252	0.0052	0.0050	0.0690	0.0132	0.0142
R8C1	0.00165	0.00015	0.00028	0.0288	0.0026	0.0050	0.0800	0.0066	0.0142

* Eight solutions of the supra-optimal series formed precipitates after standing from one to three days and are for this reason omitted from the table.

THE PLANTS AND THEIR TREATMENT

The wheat used was of the variety known as Fulcaster, from the same lot as was used by Tottingham in 1913, which was supplied by the United States Department of Agriculture. All the seed used was fairly uniform in size, and germinated well.

Germination was brought about by a modification of the methods employed by Livingston,[15] by Schreiner and Skinner,[16] by other workers in the United States Bureau of Soils, and by Tottingham. The seeds were soaked in distilled water for a period of from six to eight hours and were then placed on wet blotting paper in a moist chamber for from twelve to fifteen hours, or until they germinated. Uniform and vigorously germinated seeds were then selected, one by one, from the lot, and were placed upon the germination net, to grow till large enough for the culture bottles.

This net is constructed as follows: A glass rod, 5 mm. in diameter, is bent to form a square frame, with one end of the rod continued to form a diagonal across the square. This frame is placed between two layers of paraffined mosquito netting, and the whole rests upon the top of a circular "graniteware" pan (35 cm. in diameter and 7 cm. deep) with the corners of the frame resting on the slightly projecting rim. The two pieces of netting are firmly stretched over the top of the pan and over the frame by binding beneath the marginal rim of the pan with a heavy cord. The top layer of netting upon which the germinating seeds are to be placed, is thus raised about 5 mm. above the top of the pan, while the lower net is nearly parallel to the upper and about 5 mm. below it. While water is allowed to flow into the pan and overflow, the water surface comes into contact with the upper net, but does not completely flood the seeds, which are always in contact with water, and still freely exposed to the atmosphere.

The pan with the germinating seeds stood in a greenhouse room, and a stream of tap water was allowed to flow into the pan continuously, through a small-bore glass tube that penetrated the double net. After three or four days, this procedure resulted in very uniform and vigorous seedlings about 5.5 cm. tall and entirely free from fungus. Flowing tap water seemed to yield better results than could be obtained by the use of distilled water, even with frequent changes, as was, indeed, to be expected, on account of the extraction or leaching effect always produced by distilled water. The double net is necessary for buckwheat, but the lower one may be omitted for wheat.

Selected seedlings, from 5 to 6 cm. tall, were mounted in thoroughly paraffined, flat cork stoppers (in a manner similar to that described by Tottingham, pages 173–175), which were then placed in the culture

[15] Livingston, B. E., A simple method for experiments with water cultures. Plant World 9: 13–16. 1906.

[16] Schreiner, O. and Skinner, J. J., Some effects of a harmful organic soil constituent. U. S. Dept. Agric. Bur. Soils Bull. 70. 1910.

bottles. The latter were wide-mouth flint-glass bottles of 250 cc. capacity. These had been in use as culture vessels for several years, so that the absence of excessive amounts of soluble matter at the inner surface of the glass was assured.

In water culture work, the glass culture vessels are sometimes covered with black paper or other black material, to exclude light from the roots of the plants. This practice is particularly objectionable when cultures are exposed to direct sunlight, since the rate of heat absorption by the black material is often sufficient to raise the temperature of the culture solutions considerably above that of the surroundings—a complication to be avoided as far as possible. In the present work, the culture vessels were covered with shells or jackets of Bristol board, which was dark brown on one side and nearly white on the other. To make these shells, rectangular pieces of Bristol board were cut sufficiently long to wrap around the culture bottle, with some overlapping; the pieces were about 1.5 cm. greater in width than the height of the bottle. One long edge of this rectangle was folded over so as to form a projection about 1.5 cm. wide, perpendicular to the remaining part. This projecting portion was slashed across from its free edge, at intervals of about 1.5 cm., so as to allow the cut edges to overlap when the main portion was wrapped about the culture bottle. When this cylindrical shell, which was dark within and almost white without, was in place, the horizontal upper rim slightly overlapped the edge of the cork stopper in the mouth of the bottle. Light was thus almost completely excluded from the roots of the seedlings, and undue absorption of heat was avoided. These shells were held in place by a cord fastened around the outside; they could be easily and quickly removed from the culture bottles at any time, and replaced again without disturbing the cultures. With proper care, such shells may be used repeatedly.

The seedlings were mounted in the cork stoppers and placed in the culture bottles as rapidly and as carefully as possible, so that effects incident to handling should be approximately the same on all the seedlings, and the shock of transfer should be reduced to a minimum.

In studying the physiological effects of nutrient solutions it is always recognized as desirable to control all conditions affecting the organisms excepting those directly dependent upon the properties of the solutions, but this has never yet been satisfactorily accomplished. If aerial conditions can not be kept constant, it is clearly essential that all the cultures of a series be exposed to these conditions in an approximately similar way, so that all of the cultures shall experience the same variations in the surroundings. The cultures of a series are usually exposed by being placed side by side in some definite arrangement, upon a table or bench, the arrangement being sometimes changed from time to time. The aerial conditions affecting the plants may vary widely, however, within the area occupied by such an

arrangement of cultures, and they do not all experience the same environmental changes. For example, cultures are almost certain to shade each other, some thus receiving more light than others, and cultures entirely surrounded by other cultures are undoubtedly subjected to a lower degree of atmospheric evaporating power than those not so surrounded. These undesirable inequalities of treatment were avoided in the present work by placing all the cultures upon two rotating tables, which stood side by side in the greenhouse.

The rotating tables here employed are constructed in the following manner. A motor-cycle wheel is mounted in a horizontal position upon a heavy, iron tripod-base, especially constructed for the purpose and having a radius of 53 cm. The wheel is provided with a special axle, extended at one end beyond the cone, to form a projecting piece 5 cm. in length and 2.2 cm. in diameter. This projection is tightly fitted into a suitable opening in the center of the tripod. Upon the wheel thus mounted, rests a circular wooden platform 1.2 meters in diameter, which is firmly secured by screws through the rim of the wheel. The platform itself is three-ply, with the grain of the wood crossed, and it is further prevented from warping by radial cleats bolted to its lower surface, and by its attachment to the rim. Such tables are easily capable of supporting a weight of 150 pounds, distributed uniformly about the center.

The tables were rotated by a small electric motor, belted to a reducing gear, which, in turn, was belted to the table. The belt connecting the first table to the reducing gear and also that joining the two tables were applied directly to the rims of the motor-cycle wheels. Each table made one complete revolution in about four minutes, thus exposing all the cultures to approximately similar changes of light, heat, and moisture conditions. The tables containing the cultures were rotated continuously during the entire time of an experiment, excepting that they were stopped for a short period every three days to allow the solutions to be changed.

The three series of wheat cultures here considered were conducted simultaneously for a period of twenty-three days after the plants were placed in the nutrient solutions. The nutrient solutions were renewed every third day. Each cork stopper, with its plants, was removed from its bottle and was transferred, as quickly and as carefully as possible, to another bottle containing the new solution. The used culture solution was discarded, after its volume had been determined. The original amount of solution (250 cc.) minus the amount remaining in a culture bottle when the solution was changed was, of course, a measure of the absorption (and approximately of the transpirational loss) for the culture in question and for the given time period. Data of the total transpirational water loss for each culture for the entire growth period, as well as for the partial periods between each two changes of solutions, were thus obtained. The used culture bottles were

thoroughly cleaned, being rinsed first with tap water and then with distilled water, before each new filling.

During the period of growth, the general character of the development of tops and roots, as well as any unusual phenomena occurring in the plants, were noted. At the end of an experiment, the tops of the plants were severed from the roots just above the remains of the seed. The tops and roots were then dried separately in an electric oven at a temperature of from 75° to 80°C., for a period of about twenty-four hours, after which they were dried to constant weight at a temperature of from 102° to 104°C. The weighing bottles were transferred from the oven to a desiccator and were allowed to cool before weighing.

Records of temperature and of the evaporating power of the air in the greenhouse room where the cultures were carried out, were kept throughout the experiments. Temperature changes were recorded by means of a thermograph protected from direct sunlight and standing beside the rotating tables. The evaporating power of the air was measured by means of standardized porous cup atmometers;[17] several of these instruments were placed among the cultures on the rotating tables and daily readings were taken. Readings were corrected by multiplying by the coefficient of correction of the cup used.[18] The cups were frequently restandardized, but no marked alteration in the coefficients was detected, although the cups were not cleaned throughout the entire period of operation.

The first series of cultures was conducted in September, 1914, and this was repeated in November.

RESULTS AND SPECIAL DISCUSSION

1. INTRODUCTORY

Each of the two triple series of cultures here considered extended over a time period of twenty-three days. Series A, sub-optimal, optimal, and supra-optimal concentrations, was carried out between September 8 and October 1, 1914. Series B was exactly like series A but was carried out between November 13 and December 6. During the period of series A, the maximum temperature experienced by the cultures was 32°C. (on September 23) and the minimum was 12°C. (on September 29). The water loss from the porous cup atmometer, indicating the evaporating power of the air, gave a daily mean of 7.7 cc., a maximum daily rate of 14.3 cc. (on September 16), a minimum daily rate of 3.4 cc. (on September 12), and a total loss from the instrument of 177 cc. for the entire time period. During the growth period of series B a

[17] Livingston, B. E., Atmometry and the porous cup atmometer. Plant World **18**: 21–30, 51–74, 95–111, 143–149. 1915. Also reprinted, Tucson, 1915. (This paper gives numerous references to the earlier literature of the instrument.)

[18] The cups used were obtained from the Plant World, Tucson, Arizona.

maximum temperature of 28°C. occurred on November 23, and a minimum of 13°C. was reached on November 18. The evaporation rate from the atmometer gave a daily mean of 10.8 cc., a maximum daily rate of 14.2 cc. (on December 4), a minimum daily rate of 10.4 cc. (on November 30), and a total loss from the instrument of 248 cc. for the entire time period. These atmometer readings are all corrected to the Livingston cylindrical standard.

The present section will deal with the growth of the plants in the various cultures, as showing the physiological effects produced by the different total concentrations and the different salt proportions. The responses of the plants to the solution in which they grew will here be studied by means of three kinds of plant measurements, two of them strictly quantitative and the other more qualitative. The most useful quantitative measurements are in terms of the dry weights obtained from the cultures at the end of the period of growth. The more qualitative comparisons are made in terms of the apparent condition of the plants at the end of the culture period, and they deal mainly with unusual or pathological conditions as these might be detected by general observation. Finally, the second quantitative method of comparing the plants of the various cultures is by means of the relative amounts of water lost by transpiration during the entire culture period. These transpiration values will be considered in connection with the corresponding dry weights, to give the water requirements of the different cultures.

The results obtained by these three methods of study will be set forth in order.

2. DRY WEIGHTS

A. Presentation of dry weight data for tops and roots

Since the tops and roots were weighed separately, there are two sets of dry weight measurements available for each culture, both of which are of great interest. Also, by summing these two weights the total dry weight of any culture (six plants) may be obtained. Since, however, these sums are so markedly dominated by the dry weights of tops, they are of comparatively little interest here, and need not be further considered.

The numerical data of the yields of tops and of roots are presented in tables III, IV, and V. Each of these tables gives the dry weights of tops and of roots for series A and B, for a single one of the three total concentrations here employed. The first column gives the culture numbers, corresponding to their positions on the triangular diagram showing the variations in salt proportions (fig. 1). Then follow three columns referring to tops and three referring to roots. The first two columns in each of these groups of three present the data for series A and B, respectively, and the third column in each group gives the numbers obtained by averaging the corresponding data from series A and B. Each of these averages thus represents the two series combined. Each of the data is expressed in terms of the corresponding datum

TABLE III

Relative dry weights of tops and roots of wheat grown 23 days in three-salt solutions having sub-optimal total concentration (0.1 atm.); series A conducted from September 8 to October 1, series B, from November 13 to December 6, 1914.

CULTURE NUMBER	TOPS (6 PLANTS)			ROOTS (6 PLANTS)		
	Series A	Series B	Average	Series A	Series B	Average
R1C1	1.00* (0.2454)	1.00 (0.2748)	1.00L (0.2601)	1.00* (0.0948)	1.00 (0.1088)	1.00 (0.1036)
C2	1.32	1.11	1.22	1.13	0.97	1.05
C3	1.30	1.20	1.25	1.11	0.87	0.99
C4	1.25	1.34	1.30	0.87	0.95	0.91
C5	1.37	1.10	1.24	1.01	0.70	0.86L
C6	1.42	1.33	1.38	1.09	0.87	0.98L
C7	1.27	1.22	1.25	0.87	0.69	0.78L
C8	1.38	1.08	1.23	0.94	0.66	0.80L
R2C1	1.09	0.97	1.03L	1.27	1.11	1.19
C2	1.24	1.16	1.20	1.05	1.03	1.04
C3	1.47	1.31	1.39	1.00	0.85	0.93
C4	1.58	1.38	1.48	1.05	0.82	0.94
C5	1.38	1.42	1.40	0.80	0.73	0.77L
C6	1.40	1.46	1.43	0.78	0.73	0.76L
C7	1.47	1.30	1.39	0.97	0.62	0.80L
R3C1	1.27	0.94	1.11L	1.60	1.17	1.39H
C2	1.34	1.22	1.28	1.23	1.14	1.19
C3	1.47	1.37	1.42	0.96	1.04	1.00
C4	1.63	1.51	1.57H	0.95	0.92	0.94
C5	1.54	1.49	1.52H	0.93	0.70	0.82L
C6	1.60	1.10	1.35	0.97	0.85	0.91
R4C1	1.04	0.95	1.00L	1.45	1.17	1.31H
C2	1.33	1.09	1.21	1.35	1.09	1.22H
C3	1.49	1.33	1.41	1.23	0.88	1.06
C4	1.52	1.62	1.57H	0.82	0.95	0.89L
C5	1.66	1.63	1.65H	1.01	0.76	0.89L
R5C1	1.19	0.99	1.09L	1.36	1.23	1.30H
C2	1.35	1.58	1.47	1.25	1.11	1.18
C3	1.50	1.31	1.41	1.04	0.76	0.90
C4	1.32	1.31	1.32	0.75	0.68	0.72L
R6C1	1.25	0.95	1.10L	1.48	1.13	1.31H
C2	1.45	1.13	1.29	1.07	1.07	1.07
C3	1.52	1.36	1.44	1.19	0.85	1.02
R7C1	1.26	0.96	1.11L	1.52	1.19	1.36H
C2	1.38	1.20	1.29	1.40	1.16	1.28H
R8C1	1.24	0.96	1.10L	1.53	1.17	1.35H
K**	1.24	1.46	1.35	0.98	0.78	0.88
T**	1.62	1.61	1.62	0.92	0.91	0.92

* The dry weight of culture R1C1 is always taken as unity and the other weights are expressed in terms of this. The actual dry weight of culture R1C1 is given in parenthesis, in grams.

** K and T represent Knop's solution and Tottingham's best solution for wheat tops, respectively. These data are introduced for comparison.

TABLE IV

Relative dry weights of tops and roots of wheat grown 23 days in three salt solutions having optimal total concentration (1.75 atm.); series A conducted from September 8 to October 1, series B, from November 13 to December 6, 1914.

CULTURE NUMBER	TOPS (6 PLANTS)			ROOTS (6 PLANTS)		
	Series A	Series B	Average	Series A	Series B	Average
R1C1	1.00* (0.4038)	1.00 (0.4170)	1.00L (0.4104)	1.00* (0.1016)	1.00 (0.1099)	1.00 (0.1058)
C2	1.26	1.12	1.19	1.26	0.95	1.11H
C3	1.10	1.29	1.20	0.90	0.96	0.93L
C4	1.21	1.12	1.17	1.11	1.02	1.07H
C5	1.24	1.27	1.26	1.02	0.95	0.99
C6	1.27	1.05	1.16	1.10	0.96	1.03
C7	1.17	1.04	1.11	1.04	0.98	1.01
C8	1.23	1.10	1.17	1.02	0.88	0.95
R2C1	1.02	1.03	1.03L	0.97	0.94	0.96
C2	1.23	1.05	1.14	1.16	0.94	1.05H
C3	1.28	1.22	1.25	1.11	0.75	0.93L
C4	1.34	1.19	1.27	1.07	0.83	0.95
C5	1.15	1.20	1.18	0.95	0.85	0.90L
C6	1.26	1.19	1.22	1.00	0.96	0.98
C7	1.33	1.13	1.23	1.17	0.90	1.04
R3C1	1.18	1.11	1.15	1.07	0.96	1.02
C2	1.29	1.19	1.24	1.21	0.93	1.07H
C3	1.38	1.34	1.36H	1.18	0.96	1.07H
C4	1.27	1.28	1.28	0.95	0.94	0.95
C5	1.23	1.27	1.25	0.93	0.90	0.92L
C6	1.23	1.31	1.27	0.94	0.91	0.93L
R4C1	1.13	1.11	1.12	1.02	1.05	1.04
C2	1.36	1.19	1.28	1.15	1.04	1.10H
C3	1.32	1.20	1.26	0.96	0.85	0.91L
C4	1.33	1.21	1.27	0.97	0.84	0.91L
C5	1.38	1.21	1.30H	1.08	1.00	1.04
R5C1	1.18	1.20	1.19	1.07	1.06	1.07H
C2	1.41	1.36	1.39H	1.14	1.01	1.08H
C3	1.30	1.17	1.24	0.97	0.85	0.91L
C4	1.37	1.18	1.28	1.10	0.95	1.03
R6C1	1.21	1.13	1.17	1.14	0.98	1.06H
C2	1.27	1.10	1.19	0.97	0.85	0.91L
C3	1.30	1.12	1.21	0.93	0.81	0.87L
R7C1	1.22	1.09	1.16	1.10	0.95	1.03
C2	1.33	1.28	1.31H	1.04	0.91	0.98
R8C1	1.23	.....	1.23	1.21	.....	1.21
K**	1.16	1.02	1.09	1.01	0.88	0.95
T**	1.22	1.32	1.27	1.08	0.96	1.02

* The weight of culture R1C1 is always taken as unity and the other weights are expressed in terms of this. The actual dry weight of culture R1C1 is given in parenthesis, in grams.

** K. and T represent Knop's solution and Tottingham's best solution for wheat tops, respectively. These data are introduced for comparison.

TABLE V

Relative dry weights of tops and roots of wheat grown 23 days in three-salt solutions having supra-optimal total concentration (4.0 atm.); series A conducted from September 8 to October 1, series B, from November 13 to December 6, 1914.

CULTURE NUMBER	TOPS (6 PLANTS)			ROOTS (6 PLANTS)		
	Series A	Series B	Average	Series A	Series B	Average
R1C1	1.00* (0.2668)	1.00 (0.3628)	1.00L (0.3598)	1.00* (0.0938)	1.00 (0.0798)	1.00L (0.0868)
C2	1.13	1.12	1.13	0.94	1.14	1.04L
C3	.....	.....	.....	.....	.....	.....
C4	.....	.....	.....	.....	.....	.....
C5	.....	.....	.....	.....	.....	.....
C6	.....	.....	.....	.....	.....	.....
C7	.....	.....	.....	.....	.....	.....
C8	0.97	1.29	1.13	0.78	1.45	1.12
R2C1	0.88	1.06	0.97L	0.99	1.21	1.10
C2	1.14	1.13	1.14	1.06	1.20	1.13
C3	1.33	1.25	1.29H	1.19	1.16	1.18
C4	.....	.....	.....	.....	.....	.....
C5	.....	.....	.....	.....	.....	.....
C6	1.27	1.33	1.30H	1.08	1.33	1.21
C7	.....	.....	.....	.....	.....	.....
R3C1	0.99	1.10	1.05	1.01	1.21	1.11
C2	1.03	1.16	1.10	1.08	1.24	1.16
C3	1.24	1.28	1.26H	1.09	1.27	1.18
C4	1.20	1.28	1.24	1.01	1.19	1.10
C5	1.26	1.25	1.26H	1.11	1.25	1.18
C6	1.18	1.09	1.14	1.19	1.29	1.24
R4C1	1.02	1.11	1.07	1.16	1.40	1.28H
C2	1.10	1.36	1.23	1.12	1.39	1.26H
C3	**1.34**	**1.42**	**1.38H**	**1.23**	**1.45**	**1.34H**
C4	1.16	1.27	1.22	1.18	1.38	1.28H
C5	1.16	1.30	1.23	1.18	1.30	1.24
R5C1	0.91	1.05	0.98L	1.14	1.42	1.28H
C2	1.14	1.27	1.21	1.18	1.30	1.24
C3	1.15	1.29	1.22	1.05	1.25	1.15
C4	1.23	1.18	1.21	1.18	1.28	1.23
R6C1	0.98	1.12	1.05	1.17	1.40	1.29H
C2	1.14	1.20	1.17	1.19	1.24	1.22
C3	1.01	1.15	1.08	1.08	1.18	1.13
R7C1	1.00	1.02	1.01L	1.22	1.25	1.24
C2	1.02	1.06	1.04	1.19	1.24	1.22
R8C1	0.94	0.86	0.90L	1.22	1.14	1.18
K**	1.09	1.00	1.05	0.97	1.02	1.00
T**	1.23	1.22	1.23	1.24	1.25	1.25

* The dry weight of culture R1C1 is always taken as unity and the other weights are expressed in terms of this. The actual dry weight of culture R1C1 is given in parenthesis, in grams.

** K and T represent Knop's solution and Tottingham's best solution, respectively. These data are introduced for comparison.

for culture R1C1, considered as unity, but the actual dry weight for this culture is given in parentheses, in grams. The actual weight, in any case, may be obtained by multiplying the relative weight by the actual weight of culture R1C1 as given in the same column. The maximum yield in each series is here indicated by black-face type. The last two items in each column give the data obtained from cultures in Knop's solution and in Tottingham's best solution for wheat tops, with total concentrations equal to that of the three-salt solution considered in the same table. As has been remarked, the supra-optimal series was not complete, on account of the instability of certain solutions. Also, culture R8C1 of optimal series B suffered an early death, for some reason not related to the properties of this particular solution; its data are therefore omitted.

In the discussion of these data the dry yields of tops will be treated first, followed by a similar treatment of root yields. For facility in making comparisons, the dry weights of tops and of roots relative to that of culture R1C1 for each actual series and for the three series of averages were plotted on triangular diagrams corresponding to that shown in figure 1. Only the three diagrams for average yields will be presented here, however (figs. 2–4 and 6–8), and only these averages will be discussed in detail. While considerable difference occurred between the two series (A and B) of each pair, these differences must be related to unknown conditions, and the most prominent features of both individual series of each pair are clearly brought out by the corresponding series of averages. (The diagrams of these figures also show the ion ratio values for the different culture solutions, which will be considered below. For the present discussion the narrow lines crossing the triangles may be ignored altogether, as well as the marginal numbers designating these lines, and also the ratio formulas.)

At the intersections showing the culture locations on the diagrams of figures 2–4 and 6–8, were placed numbers representing the relative average dry weights, taken directly from the proper columns of tables III, IV, and V. Thus each diagram represented graphically the distribution of average dry-weight magnitudes or yields in its particular series. To facilitate the study of this distribution, the total range of yields was divided into a lower one-fourth, a medium one-half, and an upper one-fourth, and three regions were outlined on each triangle, corresponding to these three partial ranges. (In tables III, IV, and V, the average yields are marked with an L if they lie within the lower one-fourth of the total range for the series, and with an H if they lie within the upper one-fourth.) The low and the high regions were then separated from the medium region by broken lines, each drawn through points showing equal values. These lines are shown in figures 2–4 and 6–8, but the yield values are omitted from the diagrams, to avoid complication. Also, the culture numbers are omitted from these triangles; they are of course the same as those shown in figure 1. One of the broken lines thus drawn

upon the triangular diagram represents the upper limit of the area of low average dry weight (thus separating the lower one-fourth from the medium one-half) and the other indicates the lower limit of the area of high average weights (separating the upper one-fourth from the medium one-half). High areas (very good growth) are indicated by crosses and low areas (very poor growth) by small circles. The position on each diagram of the culture giving the greatest average dry weight is shown by a larger circle.

B. Dry weights of tops

Inspection of the columns referring to tops in tables III, IV and V, and of the triangular diagrams of figures 2–4, brings out the fact that the yield of

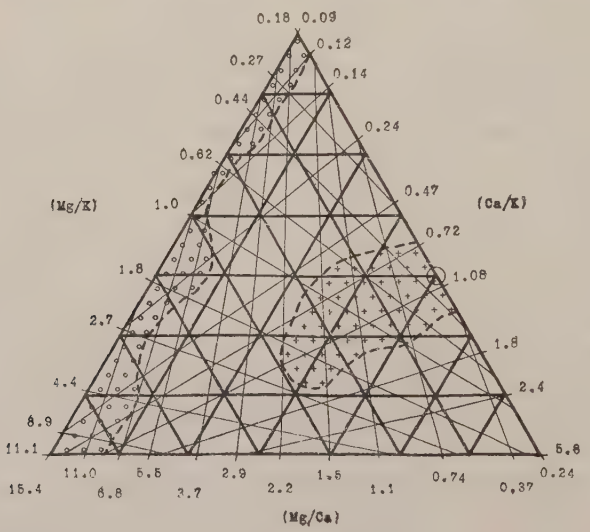

FIG. 2. Diagram showing relative yields of wheat tops in *sub-optimal* total concentration (0.1 atm.), averages from series A and B. Area of low yields (1.00 to 1.16) indicated by small circles; area of high yields (1.49 to 1.65) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

tops is directly related to the total osmotic concentration and to the osmotic proportions of the salts in the culture solutions, as was of course to be expected. The following paragraphs will deal with these relations. The points to be brought out will be presented in three groups, referring to the three total concentrations employed. The discussion will proceed with reference to the triangular diagrams of figures 2–4, and will deal especially with the ranges of the high and low average dry weights, or the extents of the corresponding high and low areas as marked on the diagrams. In this study it is to be remembered that the position of any culture on the triangular diagram, and the range of any area, is a graphic representation of the osmotic proportions

of the three salts as they occur in that culture solution, or of the range of these proportions in the cultures giving high or low average dry weights of tops. To interpret these positions upon the diagrams in terms of osmotic proportions of salts reference is to be had to figure 1.

(1) *Sub-optimal total concentration (0.1 atm.) (fig. 2).* The average dry weights from sub-optimal series A and B (plotted on the diagram of figure 2) indicate an area of low average weights (1.00-1.16) including the entire row of cultures on the left margin of the triangle, while the area of high average weights (1.49–1.65) occupies the right central region.

The highest average dry yield of tops occurs with culture R4C5 and is 65 per cent higher than the corresponding average for culture R1C1. The

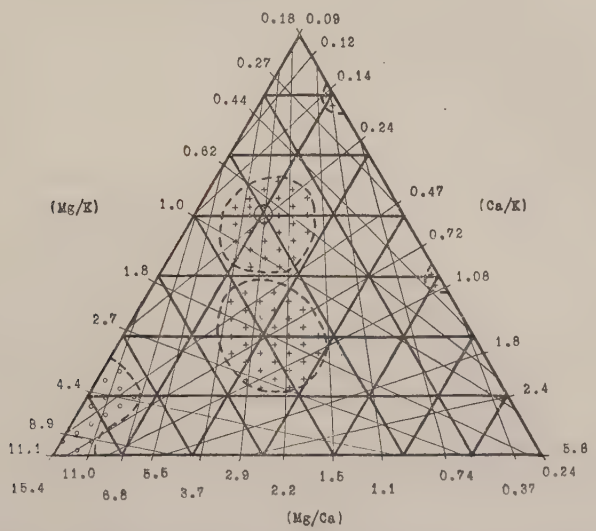

FIG. 3. Diagram showing relative yields of wheat tops in *optimal* total concentration (1.75 atm.), averages from series A and B. Area of low yields (1.00 to 1.10) indicated by small circles; area of high yields (1.29 to 1.39) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

same culture gave the highest actual yield in both series A and series B, the increase over that of culture R1C1 being 66 per cent for the first and 63 per cent for the second series. From this agreement it appears that the greatest production of dry weight of tops in this three-salt solution with 0.1 atmosphere of diffusion tension is to be expected with the salt proportions of culture R4C5. This solution is characterized by having five-tenths of its total diffusion tension due to calcium nitrate, one-tenth due to magnesium sulphate, and four-tenths due to mono-potassium phosphate.

(2) *Optimal total concentration (1.75 atm.) (fig. 3).* The diagram representing the average yields for the optimal total concentration shows an area

of low yields (1.00–1.10) at the extreme lower left. It shows two main areas of high yields (1.29–1.39) in the left central region, which are nearly joined at cultures R4C2 and R4C3. Secondary areas of high yield are also indicated for cultures R4C5 and R7C2, but these yields are not relatively very high.

Optimal series A and B agree in showing the highest dry weight of tops for the same culture, R5C2. In series A the yield for this culture was 41 per cent, and in series B 36 per cent higher than the corresponding dry yield for culture R1C1. The highest average yield of tops, of course, also occurs for culture R5C2, and is 39 per cent higher than the average yield for culture R1C1. It thus appears that the greatest production of dry weight of tops

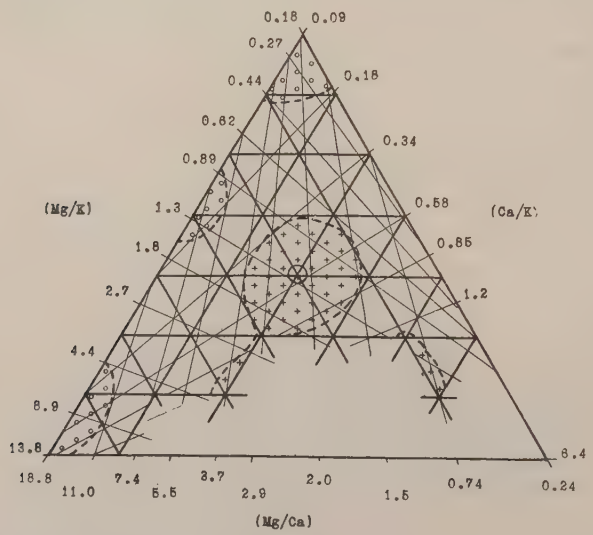

FIG. 4. Diagram showing relative yields of wheat tops in *supra-optimal* total concentration (4.0 atm.), averages from series A and B. Area of low yields (0.90 to 1.02) indicated by small circles; area of high yields (1.26 to 1.38) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

in this three-salt solution with 1.75 atmospheres of total diffusion tension is to be expected with the salt proportions of solution R5C2. This solution is characterized by having two-tenths of its total diffusion tension due to calcium nitrate, three-tenths due to magnesium sulphate, and five-tenths due to mono-potassium phosphate.

(3) *Supra-optimal total concentration (4.0 atm.) (fig. 4).* The incompleteness of the supra-optimal series, on account of the instability of some of the solutions, renders the location of the high and low areas on the diagram of figure 4 somewhat unsatisfactory. It appears highly probable that the main regions of high and low dry weights of tops are here rightly indicated, however.

The area of low average yields of tops (0.90–1.02) occupies three regions at the left margin of the diagram (fig. 4), and the main area of high average yields (1.26–1.38) occupies the center of the triangle.

The highest dry weight of supra-optimal series A occurred with culture R4C3 and was 34 per cent higher than that given by culture R1C1 of the same series. Similarly, the highest dry weight of series B occurred with the same culture and was 42 per cent higher than the corresponding weight of culture R1C1. The highest average yield (culture R4C3) is 38 per cent higher than that for culture R1C1. It thus appears that the greatest production of dry weight of tops in this three-salt solution with 4.0 atmospheres of total diffusion tension is to be expected with the salt proportions of culture R4C3. This solution is characterized by having three-tenths of its total diffusion tension due to calcium nitrate, three-tenths due to magnesium sulphate, and four-tenths due to mono-potassium phosphate.

(4) *Relation of total concentration to the physiological effects of the various osmotic proportions of the salts. Consideration of relative dry weights of tops (figs. 2–4).* It is important to appreciate the effect of the total concentration of the medium in determining the relative physiological values of the various salt proportions represented in each series. This may be done by referring to the three triangular diagrams representing average dry weights of tops (figs. 2–4). The positions and ranges, on these diagrams, of the areas of low and high average dry weights, and the positions of the solutions showing maximum yields, as these positions and ranges are altered relative to the total concentration, will now receive attention.

In passing from the sub-optimal to the optimal series (from fig. 2 to fig. 3), it is seen at once that the extent of the area of low top yields becomes greatly reduced. While this area extends along the entire left margin of the diagram representing the sub-optimal series (fig. 2), it is restricted to a small region at the lower left in the diagram representing the optimal (fig. 3). While eight solutions lie within this area on the sub-optimal diagram, only two (R1C1 and R2C1) are thus included on the other. Nevertheless, it is to be noted that these two solutions, the dry weights for which lie within the lower one-fourth of the total range of these weights for the optimal series, are the same solutions (characterized by the same salt proportions) that show the lowest two dry weights in the sub-optimal series. It is to be noted further, that the remaining left-marginal solutions of the optimal diagram (fig. 3) are all characterized as giving very low medium weights. These two total concentrations thus agree in indicating solutions R1C1 and R2C1 as very poorly adapted to the production of dry weights of tops of wheat as here grown. They also agree in showing the entire left marginal row of solutions on the triangular diagram as physiologically poor.

Turning to the supra-optimal diagram (fig. 4), the area of low top yields appears here in three separate portions lying at the left margin of the triangle,

and the marginal solutions that lie between these separate portions of the area of low yields show very low medium weights. Thus the solutions of the left marginal row are indicated as of poor physiological balance for all three concentrations. In the supra-optimal series, solutions R1C1 and R2C1 (which show the two lowest yields in both of the other two series, as has been noted) do not show the lowest yields, but the next to the lowest is here given for one of these two, R2C1 (0.97).

It is apparent that some differences are manifest between the physiological properties of the left marginal solutions, according to the total concentrations, but these differences are not greatly marked. These eight solutions are characterized by low osmotic partial concentrations of calcium nitrate, but they include the whole range of partial concentrations in the case of both of the other salts. The worst two solutions (R1C1 and R2C1) are characterized by low partial concentrations of mono-potassium phosphate and high partial concentrations of magnesium sulphate. It thus appears that physiological balance is greatly disturbed by low partial concentration of the calcium salt, and this disturbance tends to be aggravated by relatively high partial concentrations of magnesium sulphate accompanied by low ones of mono-potassium phosphate.

Turning now to the areas of high relative dry weights, as represented on the diagrams of figures 2–4, if we pass from the sub-optimal to the optimal triangle (from fig. 2 to fig. 3), it appears as though the high area of the former drew away from the right margin and became more centralized, also dividing into two separate portions. These two portions of the high area of the optimal diagram (fig. 3) lie mainly to the left of the central vertical axis of the triangle and do not extend to the margin at any point. Passing to the supra-optimal diagram (fig. 4), these two regions of high yields appear to become combined in a more restricted region about the center of the diagram, but the supra-optimal series is not perfectly satisfactory, on account of incompleteness due to the chemistry of the salts.

If we compare the three solutions that show highest average yields of tops in the three series, respectively, we find that the best proportions of salts are not at all the same for the three different total concentrations here tested. With the sub-optimal total concentration (fig. 2) the best physiological balance is shown for solution R4C5, which is characterized by having only one-tenth of its total diffusion tension due to $MgSO_4$ while the remaining nine-tenths of the total diffusion tension is almost equally divided between the other two salts, five-tenths being due to $Ca(NO_3)_2$ and four-tenths to KH_2PO_4. With the optimal total concentration (fig. 3), solution R5C2 shows the best yield, and this solution occupies an entirely different position on the diagram from that occupied by R4C5. This solution has a relatively low partial diffusion tension due to $Ca(NO_3)_2$ (two-tenths), and a relatively high osmotic content of $MgSO_4$ (three-tenths). With the supra-optimal total concentration (fig. 4)

the solution showing the highest dry weight of tops occupies still another position on the diagram. This solution has equal osmotic proportions of $Ca(NO_3)_2$ and $MgSO_4$, three-tenths of its total diffusion tension being due to each of these salts, and four-tenths are due to KH_2PO_4.

From these considerations it may be safely concluded, as has already been pointed out by Gile,[19] McCool,[20] and Tottingham, that physiological salt-balance in such nutrient media as these is markedly dependent upon the total concentration of the solution. It is therefore quite out of the question to state any given set of proportions of the three salts here used, that may be expected to give any particular kind of growth (as optimum, good, poor, etc.), unless the total concentration of the solution to be employed is also specified.

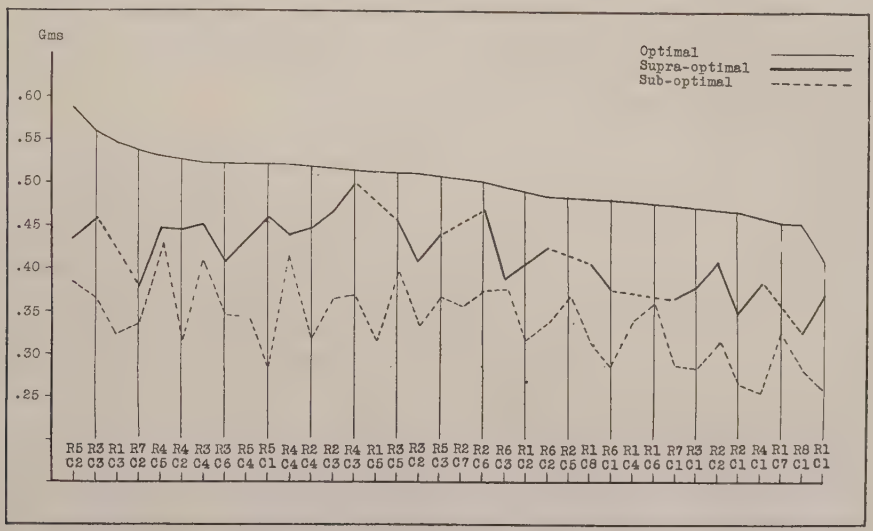
Gms
Optimal
Supra-optimal
Sub-optimal
.60
.55
.50
.45
.40
.35
.30
.25
R5 R3 R1 R7 R4 R4 R3 R3 R5 R5 R4 R2 R2 R4 R1 R3 R3 R5 R2 R2 R6 R1 R6 R2 R1 R6 R1 R1 R7 R3 R2 R2 R4 R1 R8 R1
C2 C3 C3 C2 C5 C2 C4 C6 C4 C1 C4 C4 C3 C3 C5 C5 C2 C3 C7 C6 C3 C2 C2 C5 C8 C1 C4 C6 C1 C1 C2 C1 C1 C7 C1 C1

FIG. 5. Average actual yields (grams) of wheat tops (series A and B) for sub-optimal, optimal, and supra-optimal total concentrations.

Consideration of absolute dry weights of tops. The effect of the total concentration of the medium upon the influence of various salt proportions, as these determine physiological properties, may be brought out in another way, by considering the actual dry weights instead of the relative ones treated above. To bring out the relations in question the average yields of tops for the optimum concentration were arranged in the order of their magnitudes, beginning with the highest. These form a rather uniformly decreasing series of numbers, which were next plotted to form the graph shown as the upper one in figure 5. Here the abscissas are taken arbitrarily to represent the

[19] Gile, P. L., Lime-magnesia ratio as influenced by concentration. Porto Rico Agric. Exp. Sta. Bull. 12. 1912.

[20] McCool, M. H., The action of certain nutrient and non-nutrient bases on plant growth. Cornell Agric. Exp. Sta. Mem. 2: 121-170.

different cultures, the numbers of which are placed below, and the ordinates represent the average dry weight values. With the same abscissas, the corresponding dry weight values for the sub-optimal and supra-optimal concentrations were then plotted on the same sheet, using the same scale for the ordinates. As is shown in figure 5, there result three graphs, which lie one above the other. The upper one, representing the actual average yields of the optimal series, exhibits a uniform downward slope to the right, as was previously arranged. Next below this comes the supra-optimal graph, and that for the sub-optimal series is lowest.

From figure 5 it is at once clear that the supra-optimal and sub-optimal graphs, while showing a general downward slope to the right, are very irregular and not at all parallel to each other or to the optimal graph. This indicates again that the same set of salt proportions (denoted by the same culture number) has very different physiological properties with the three different total concentrations.

Furthermore, the optimal series definitely exhibits the greatest average absolute dry weight for every set of salt proportions throughout the entire series. There is no crossing of the graphs; every set of salt proportions in the supra-optimal series gave a lower dry weight average than did the same proportions in the optimal, and every one in the sub-optimal gave a lower average weight than did the same set in the supra-optimal. The fact that each series has its own particular set of optimal proportions of the three salts is again apparent in this series of graphs. It may be added that the highest yield for the optimal concentration is not equalled by the highest one for the supra-optimal, and that the highest for the supra-optimal is not equalled by that for the sub-optimal.

Relation of yields of tops to the proportions of the chemical ions. a. Ion ratios. In connection with the problems of salt antagonism and the physiological balance of nutrient solutions, considerable attention has been given by various writers to the ratios of partial salt (ion, element, etc.) concentrations. Such ratios are frequently stated in such a way as to show the number of atoms of one element occurring in the solution, for each single atom of another element, as in the case of Loew's[21] ratio of magnesium to calcium. Of course these ratios, like the partial concentrations from which they are derived, may also be expressed directly in terms of weight, thus giving the number of grams of one element present in the solution for a single gram of another element. But this sort of expression is practically without either chemical or physiological meaning, and therefore the weight method will not be here employed. It is obvious that the cations here dealt with are atoms, while the corresponding anions are atomic groups. It therefore follows that ratios

[21] Loew, O. and May, D. W., The relation of lime and magnesia to plant growth. U. S. Dept. Agric. Bur. Plant Ind. Bull. 1. 1901.

of atoms and also those of atomic groups may be employed to characterize a given nutrient solution. Since ions are to be considered as the chemically and metabolically active units in such solutions as those here dealt with, a detailed study of ionic ratios has been carried out, with the aim of finding out whether certain ones of these various ratio values may be important in determining the physiological properties of the various salt combinations. The present section will be devoted to such a study.

In the solutions here dealt with there are three cations and three anions, neglecting the very small amount of iron which is uniformly present. It follows that there are three possible cation ratios, Mg/Ca, Mg/K, and Ca/K, and their reciprocals, the latter not requiring special attention; also, there are three anion ratios, SO_4/NO_3, SO_4/PO_4, and NO_3/PO_4, and their reciprocals. This consideration neglects the H-ions that arise from KH_2PO_4, and assumes complete ionization of all the salts. From the nature of the salts used it is clear that the ratio SO_4/NO_3 always has a value just one-half as great as that of the ratio Mg/Ca for the same solution. Similarly, the ratio NO_3/PO_4 has twice the magnitude of the ratio Ca/PO_4, and the ratio SO_4/PO_4 is identical in value with the corresponding ratio Mg/K in the same solution. These relations follow from the fact that for every ion of Ca there are two ions of NO_3, while the ions of Mg and K are accompanied by single ions of SO_4 and PO_4, respectively. From the way in which these three-salt nutrient solutions are prepared, if the values of two out of the three cation ratios are known the value of the third may be found, since the total salt concentration of the solution is also known and only three salts ever enter into its composition. A similar relation holds for the magnitudes of the three anion ratios, and since these are definitely related to the cation ratio values, it follows that if the values of any two cation ratios or of any two anion ratios be given (of course not including both of any pair of reciprocals, which are really the same ratio), all the other ionic ratios may be directly calculated, including those formed from one cation and one anion.

The chemical nature of each of the solutions used in this study being thus determined by any two ion ratio values, taken together with the total concentration, it becomes of considerable importance to determine the ratios for all of the different solutions of each of the three series and to study these values with reference to the physiological properties of the various solutions.

On account of the known relations holding between the different ratio values, as noted above, it becomes unnecessary to determine any but the three different cation ratios for each solution. These determinations are accomplished by calculation directly from the partial molecular salt concentrations given in table II. Thus, in the case of solution R1C1 with optimal total concentration, for example, the partial molecular concentration of $MgSO_4$ is 0.0400, that of $Ca(NO_3)_2$ is 0.0026, and that of KH_2PO_4 is 0.0036, from which is appears that this solution contains, per liter, 0.0400 gram-ions (or gram-

atoms) of Mg; 0.0026 gram-ions of Ca, and 0.0036 gram-ions of K. The three cation ratio values characterizing this solution are then obtained by performing the operations indicated by the ratios themselves: $\frac{Mg}{Ca} = \frac{0.0400}{0.0026} = 15.40$; $\frac{Mg}{K} = \frac{0.0400}{0.0036} = 11.10$, etc. These operations are of course justified by the chemical principle (based on the atomic theory of matter) that the number of atoms of an element present in a given mass of it is proportional to the number of gram-atoms contained in the mass, a gram-atom (similar to a gram-molecule) being the number of grams of the element in question that is represented by its atomic weight.

b. Presentation of ion ratio values. The ratio values, Mg/Ca, Mg/K, and Ca/K, for all the thirty-six sets of salt proportions and for all three total concentrations here studied, are set forth in table VI. It will be noted that the ratio values are the same for the sub-optimal and optimal concentrations, but that the supra-optimal concentration has a series of its own. This is on account of the apparent depression of ionization occurring in the stronger solutions, as has been noted above. The first column of table VI gives the solution numbers, denoting the salt proportions on the basis of partial diffusion tensions. Columns 2, 3 and 4 present the three ratio values for the sub-optimal and optimal concentrations, and columns 5, 6 and 7 give those for the supra-optimal. The solutions giving the greatest yields of tops and of roots are designated in the table by letters, which refer to notes below to this effect.

The data of table VI were plotted upon the triangular diagrams, in a manner similar to that in which the dry weights were plotted, after which lines were drawn through approximately equal ratio values, thus dividing the triangular area into strips with reference to each ratio. The diagrams thus obtained have been represented by the narrow lines in figures 2–4, and will be similarly employed in figures 6–8 and in figures 10 and 11, as bases on which the other data are plotted. It will be noted, from the figures just mentioned, that the cation ratio diagram for the sub-optimal and that for the optimal total concentration (figs. 2, 3, 6, 7) are identical, while the corresponding diagram for the supra-optimal concentration (figs. 4 and 8) is somewhat different, corresponding to the fact that each cation ratio of table VI has a different value for the sub-optimal and optimal series from that given for the supra-optimal series. As has been remarked, this is due to the depressed ionization in the more concentrated series of solutions. In these figures the narrow lines approximately represent the respective ratio values, while the broad lines show by their intersections the different osmotic salt proportions and the locations of the different cultures or solutions. Since there are three ratios to be considered, there are three sets of ratio lines shown on each triangle. Each side of the triangle is intersected by all of the lines

TABLE VI

Values of the three cation ratios for three-salt solutions with sub-optimal, optimal, and supra-optimal total osmotic concentration.

SOLUTION NUMBER	SUB-OPTIMAL AND OPTIMAL CONCENTRATION			SUPRA-OPTIMAL CONCENTRATION		
	Mg/Ca	Mg/K	Ca/K	Mg/Ca	Mg/K	Ca/K
R1C1	15.40	11.10	0.72	18.80	13.78	0.73
C2[a]	6.74	9.72	1.44	8.10	11.89	1.47
C3	3.85	8.34	2.16	.....	.....	.....
C4	2.40	6.95	2.88	.....	.....	.....
C5	1.54	5.55	3.60	.....	.....	.....
C6	0.96	4.17	4.32	.....	.....	.....
C7	0.55	2.78	5.04	.....	.....	.....
C8	0.24	1.39	5.76	0.24	1.58	6.40
R2C1	13.46	4.86	0.36	16.21	5.99	0.37
C2	5.77	4.17	0.72	6.73	4.95	0.75
C3	3.21	3.47	1.08	3.60	3.95	1.10
C4	1.92	2.77	1.44	.....	.....	.....
C5	1.15	2.08	1.80	.....	.....	.....
C6	0.64	1.39	2.16	0.68	1.58	2.31
C7	0.27	0.69	2.52	.....	.....	.....
R3C1[b]	11.55	2.78	0.24	13.46	3.30	0.24
C2	4.81	2.32	0.48	5.40	2.64	0.49
C3	2.56	1.85	0.72	2.88	2.11	0.73
C4	1.44	1.39	0.96	1.61	1.59	0.98
C5	0.77	0.93	1.20	0.86	1.05	1.22
C6	0.32	0.46	1.44	0.34	0.52	1.54
R4C1	9.61	1.74	0.18	10.89	1.94	0.18
C2	3.85	1.39	0.36	4.32	1.55	0.36
C3[c]	1.92	1.04	0.54	2.16	1.16	0.54
C4	0.96	0.69	0.72	1.07	0.77	0.72
C5[d]	0.38	0.35	0.90	0.43	0.39	0.90
R5C1	7.70	1.11	0.14	8.63	1.24	0.14
C2[e]	2.88	0.83	0.29	3.24	0.93	0.29
C3	1.28	0.56	0.43	1.44	0.62	0.43
C4	0.48	0.28	0.58	0.54	0.31	0.58
R6C1	5.77	0.69	0.12	6.49	0.74	0.11
C2	1.92	0.46	0.24	2.16	0.49	0.23
C3	0.64	0.23	0.36	0.72	0.24	0.34
R7C1	3.85	0.40	0.10	4.32	0.41	0.09
C2	0.96	0.20	0.20	1.07	0.20	0.19
R8C1	1.92	0.18	0.09	2.15	0.18	0.09

[a] Best solution for yield of roots, optimal concentration.
[b] Best solution for yield of roots, sub-optimal concentration.
[c] Best solution for yield of tops and roots, supra-optimal concentration.
[d] Best solution for yield of tops, sub-optimal concentration.
[e] Best solution for yield of tops, optimal concentration.

for just one ratio and by some of the lines for each of the other two ratios. The ratio values represented by the lines of each set are shown along that side of the triangle which is intersected by all of that particular set, and that side may be considered as the triangle base for the ratio in question. The three ratio formulas are placed just outside of the triangle, on the three sides that are their respective bases, Mg/Ca being below, Mg/K at the left, and Ca/K at the right. It will be noticed at once that the ratio values do not alter at a constant rate, proceeding across the triangular diagram, so that the scale represented by the spacing of the narrow lines is much larger at one end of each series of values than at the other. In this respect the ratio diagrams are fundamentally different from those of osmotic salt proportions, represented by the broad lines of the same figures.

c. Relation of ion ratio values to yields of tops. A study of the relations between the various ion ratio values and the magnitudes of the corresponding yields, shown in figures 2–4, brings out some interesting points. In the diagram for the sub-optimal series (fig. 2) the area of low top yields, extending along the left side of the triangle embraces the full range of the value of the ratio Mg/K, from 0.18 to 11.10. The magnitude of this ratio is therefore not at all related to the production of low top yields in this series. Each of the other two ion ratios, however, shows a definite relation to the position and extent of this low area, which embraces ratio values of Mg/Ca varying from 1.62 to 15.40, and of Ca/K varying from 0.09 to 1.21. The total range of each of the last two ratios is considerably greater than the range embraced by the low area of the diagram, so that there occurs a range of ratio values, in each case, that are characterized as *not* producing low top yields. It therefore follows that low top yields are to be expected, with this sort of 3-salt solution having a total concentration of 0.1 atmosphere, when the value of Mg/Ca lies between 1.62 and 15.40 while the value of Ca/K lies between 0.09 and 1.21. The cultures giving low yields of tops are characterized as including all but the very lowest values of Mg/Ca here tested and as restricted to the lowest values of Ca/K.

Similarly, for the area of high dry weights of tops, with the sub-optimal total concentration (fig. 2), this area is seen to be confined to ratio ranges as follows: Mg/Ca, 0.38–2.36; Mg/K, 0.31–2.58; and Ca/K, 0.65–1.43. These ranges are not very great in any case, and all lie near—but do not include—the lowest values of the respective ratios occurring in the series as here arranged. Since any two ratio values are sufficient to determine the position of a point on the triangular diagram, it may be said that high top yields may be expected in this series of solutions (0.1 atm. total concentration), when the value of Mg/Ca lies between 0.38 and 2.36, and that of Ca/K lies between 0.65 and 1.43. As the series is here arranged the similar range of the third ratio value (Mg/K) is also determined by these data.

The highest average yield of tops here occurred (culture R4C5) with the

ratio values: Mg/Ca, 0.38; Mg/K, 0.35; and Ca/K, 1.08. This means that this best solution for tops contains 0.38 atom of Mg for 1 atom of Ca, 1.08 atom of Ca for 1 atom of K, and 0.35 atom of Mg for 1 atom of K. It thus contains the atoms Mg, Ca, and K in the proportions 0.35 : 1.08 : 1.00.

The remaining two diagrams of top yields (figs. 3 and 4) may be treated in a similar manner, thus bringing out the ranges of the various ratio values embraced by the low and high areas, respectively. The results of such comparisons are brought together in table VII. This table is divided into four parts. In the first part are given the minimum and maximum ratio values

TABLE VII

Minimum and maximum values for the three cation ratios, and ranges of these values, for each entire series and for high and low yields of wheat tops, with each total concentration tested. Also, these ratio values for the three best solutions for yields of tops.

		Mg/Ca RATIO			Mg/K RATIO			Ca/K RATIO		
		Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)	Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)	Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)
Entire series	Minimum	0.24	0.24	0.24	0.18	0.18	0.18	0.09	0.09	0.09
	Maximum	15.40	15.40	18.80	11.10	11.10	13.78	5.76	5.76	6.40
	Range	15.16	15.16	18.56	10.92	10.92	13.60	5.67	5.67	6.31
Low yields	Minimum	1.62	7.36	1.23	0.18	3.56	0.18	0.09	0.29	0.09
	Maximum	15.40	15.40	18.80	11.10	11.10	13.78	1.21	1.08	0.85
	Range	13.78	8.04	17.57	10.93	7.54	13.61	1.12	0.79	0.76
High yields	Minimum	0.38	1.58	0.74	0.31	0.53	0.74	0.65	0.19	0.35
	Maximum	2.36	5.16	4.07	2.58	2.84	4.45	1.43	1.45	2.31
	Range	1.98	3.58	3.33	2.27	2.31	3.71	0.78	1.26	1.96
Highest yields		0.38	2.88	2.16	0.35	0.83	1.16	1.08	0.29	0.54

and the ranges for these, for the entire series. In the second part are given the ratio values and ranges for low yields of tops (lowest one-fourth of the total range of yields). In the third part are given the corresponding numbers for high yields (highest one-fourth of the total range of yields). In the fourth part are given, for ready comparison, the ratio values characterizing the solution that produced the highest yield for each of the three different total concentrations.

The results shown in table VII are expressed graphically in figures 2–4, the first of which has been discussed. Reference to these figures and to table VII shows that the areas of low and high yields of tops are generally limited

to certain ranges of the cation ratio values, these ranges being less extensive than the corresponding total ranges for the series in question.

There are just two exceptions to this last statement; as has been remarked, the magnitude of the ratio Mg/K is without correlation to the yield of tops in the sub-optimal series (fig. 2), and the same is true for the supra-optimal series (fig. 4). Also, the range of Mg/K that defines the area of low top yields in the optimal series (fig. 3) embraces somewhat more than the upper one-half of the total range of this value in this case, so that here also, this ratio does not appear to furnish a very definite criterion by which to judge the physiological properties of the medium. It is also to be noted that the ranges of the ratio Mg/Ca that correspond to the areas of low top yields in the sub-optimal (fig. 2) and supra-optimal (fig. 4) series are almost coextensive with the corresponding total ranges for the respective series and that the range, of this same ratio value, that limits the low yields in the optimal series (fig. 3), embraces almost the whole of the upper one-half of the corresponding total range. From these observations it appears that the solutions giving low dry weights of tops are not very satisfactorily defined in terms of either the Mg/Ca or the Mg/K ratio values, though these values offer somewhat better criteria for judging the physiological balance of the solution in the case of the optimal total concentration than in either of the others.

The areas representing low yields are well defined in all three diagrams (figs. 2–4) by the ranges of the ratio-value Ca/K, this range embracing only the lower one-fifth (or less) of the corresponding total range. With all three total concentrations the solutions giving high top yields are all clearly limited to low values of all three cation ratios, but in no case are any of these solutions characterized by the very lowest ratio values here considered. In general, no single ratio and no pair of ratios appear to determine the production of high top yields any more than that of low ones.

It is instructive to observe the marked differences between the atomic proportions of Mg, Ca, and K characterizing the solutions giving the highest yields of tops in the three series, respectively. While, as has been remarked, the most perfectly balanced solution (for dry weight of wheat tops) of the sub-optimal series (total concentration 0.1 atm.) contains 0.35 and 1.08 atoms of magnesium and of calcium, respectively, for each single atom of potassium, yet the most perfectly balanced solutions of the optimal and of the supra-optimal series (total concentrations 1.75 and 4.0 atm.) are very different in this respect. The greatest yield of tops was obtained in a solution having the atomic proportions, Mg, 0.83; Ca, 0.29; K, 1.00, with optimal total concentration, while the best solution for top growth with supra-optimal total concentration possessed the proportions, Mg, 1.16; Ca, 0.54; K, 1.00. It is thus obvious that the cation atomic proportions characterizing the best physiological balance, as here brought out, vary markedly, and in no simple manner, with the total concentration of the solution.

C. Dry weights of roots

Turning now to the dry weights of roots, as given in tables III, IV, and V, it appears that these, as well as the yields of tops, show marked variations according to the osmotic proportions and total osmotic concentrations of the solutions in which they grew. The following consideration of the average root yields will follow the same general lines as were followed in considering the average weights of tops, but will not be as detailed as was the former discussion. It will have reference to the triangular diagrams of figures 6–8.

(1) *Sub-optimal total concentration (0.1 atm.) (fig. 6).* The average dry weight of roots for the sub-optimal series ranges from 0.72 to 1.39, relative to the average yield for solution R1C1. The diagram for these root yields

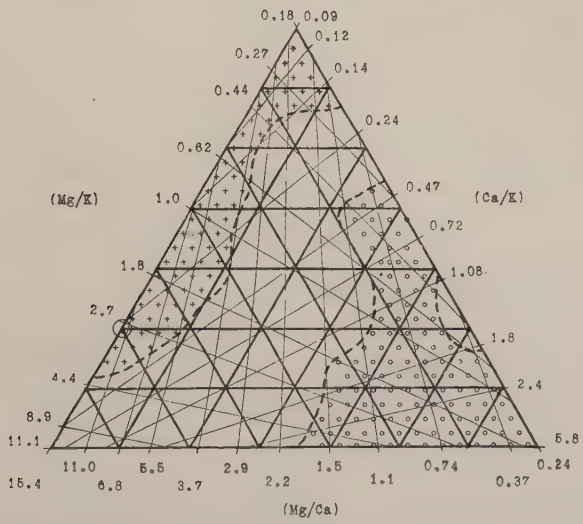

FIG. 6. Diagram showing relative yields of wheat roots in *sub-optimal* total concentration (0.1 atm.), averages from series A and B. Area of low yields (0.72 to 0.89) indicated by small circles; area of high yields (1.22 to 1.39) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

(fig. 6) shows an area of low relative values (0.72–0.89) occupying about a third of the entire triangle, about its lower right angle. The area of high root yields (1.22–1.39), on the other hand, occupies nearly the whole of the left marginal region and includes solutions R8C1 and R7C2 of the right margin. The greatest dry weight of roots for this total concentration is shown for solution R3C1, near the lower limit of the area of high root yields. This solution is characterized by having one-tenth of its total diffusion tension due to $Ca(NO_3)_2$, six-tenths due to $MgSO_4$, and three-tenths due to KH_2PO_4.

(2) *Optimal total concentration (1.75 atm.) (fig. 7).* The range of average relative root yields for the optimal series is from 0.87 to 1.11. Comparing

the diagram for this series (fig. 7) with that for the sub-optimal series (fig. 6) it appears as though the area of low relative yields had here migrated upward and to the left, while the area of high yields had correspondingly migrated downward and to the right. The main region of low dry weights of roots (0.87–0.93, fig. 7) lies mainly to the right of the central vertical axis of the triangle, but includes two solutions on that axis. The main region of high root yields (1.05–1.11) lies to the left of the central vertical axis, the greatest root yield being shown for solution R1C2 ,on the lower margin of the triangle. This solution is characterized by having two-tenths of its total diffusion tension due to $Ca(NO_3)_2$, seven-tenths due to $MgSO_4$, and one-tenth due to KH_2PO_4.

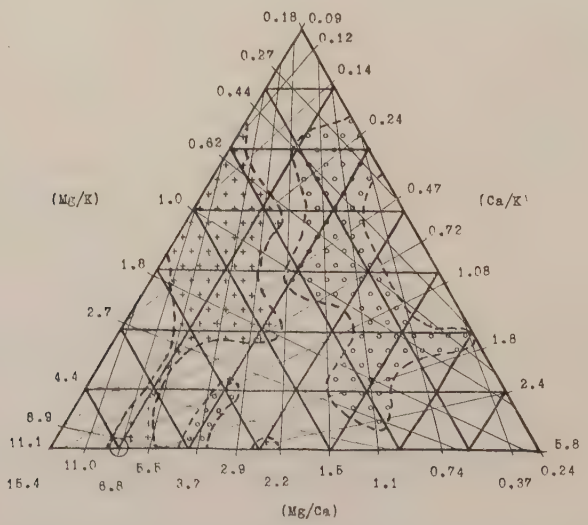

FIG. 7. Diagram showing relative yields of wheat roots in optimal total concentration (1.75 atm.), averages from series A and B. Area of low yields (0.87 to 0.93) indicated by small circles; area of high yields (1.05 to 1.11) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

(3) *Supra-optimal total concentration (4.0 atm.) (fig. 8).* The total range of average relative dry weights of roots for the supra-optimal series extends from 1.00 to 1.34. On the diagram for this series (fig. 8) the area of low average root yields (1.00–1.08) occupies the extreme lower left region of the triangle. The corresponding area of high average yields (1.26–1.34) here occupies the center of the triangle and is extended to the right, but not as far as the right margin, and also to the left, where it widens to include three solutions on the left margin. This triangle is somewhat unsatisfactory on account of its incompleteness (due to chemical relations, as has been stated), but there is no suggestion of an area of low yields at the right of the central axis (as in figs. 6 and 7), and it seems fair to suppose that the effect

of this high concentration has been to shift the region of poor growth as is here indicated. The highest average root yield is shown for solution R4C3, near the center of the diagram. This solution is characterized by having three-tenths of its total diffusion tension due to $Ca(NO_3)_2$, three-tenths due to $MgSO_4$, and four-tenths due to KH_2PO_4.

(4) *Relation of total concentration to the physiological effects of the various osmotic proportions of the salts. Consideration of relative dry weights of roots (figs. 6–8).* The effect of total concentration upon the positions and ranges of the areas of low and high average yields of roots, as shown on the triangular diagrams (figs. 6–8), will now receive attention.

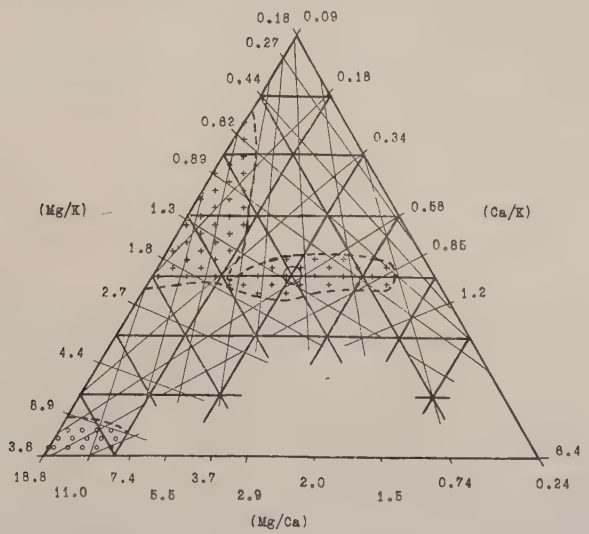

FIG. 8. Diagram showing relative yields of wheat roots in supra-optimal total concentration (4.0 atm.), averages from series A and B. Area of low yields (1.00 to 1.08) indicated by small circles, area of high yields (1.26 to 1.34) indicated by crosses. The culture giving the highest yield is marked by a larger circle.

Comparison of the diagrams of figures 6–8 makes it clear enough that total concentration has a very pronounced effect in determining the relative influence of the different salt proportions upon growth of roots as here measured. This effect is so pronounced that it is obviously impossible to select any single set of salt proportions which might agree, throughout the three total concentrations, in producing either a very low or a very high dry weight of roots. The study of the growth of roots in relation to their chemical and physical environment is in such an early stage, and the data here presented appear to be so complicated, that further generalization need not be undertaken. The point to be emphasized in this connection, as in the case of tops, is that a culture solution is not to be defined, as physiologically balanced for root

growth, in terms of its salt proportions alone; its total concentration must also be stated.

Consideration of absolute dry weights of roots. The actual average dry weights of roots obtained in a period of twenty-three days, with the various concentrations and salt proportions here studied, will now be taken up, as was done for the corresponding average yields of tops. The average dry weights of roots for the optimum concentration were arranged in the order of their magnitudes, beginning with the highest, and, as in the case of tops, these numbers form a rather uniformly decreasing series, which is shown graphically as the uniformly sloping, nearly straight line of figure 9. This graph, and the remaining two graphs of that figure, are plotted in the same

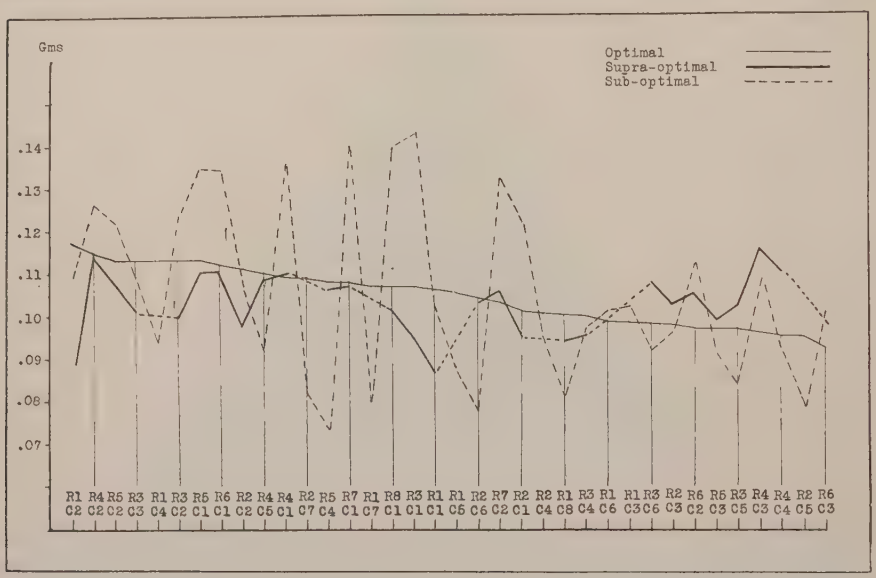
Gms
Optimal
Supra-optimal
Sub-optimal
.14
.13
.12
.11
.10
.09
.08
.07
R1 R4 R5 R3 R1 R3 R5 R6 R2 R4 R4 R2 R5 R7 R1 R8 R3 R1 R1 R2 R7 R2 R2 R1 R3 R1 R1 R3 R2 R6 R5 R3 R4 R4 R2 R6
C2 C2 C2 C3 C4 C2 C1 C1 C2 C5 C1 C7 C4 C1 C7 C1 C1 C1 C5 C6 C2 C1 C4 C8 C4 C6 C3 C6 C3 C2 C3 C5 C3 C4 C5 C3

FIG. 9. Average actual yields (grams) of wheat roots for sub-optimal, optimal, and supra-optimal total concentrations.

manner as was employed for tops (fig. 5). Unlike those for top yields, there is little or no tendency for these three graphs to show parallelism; frequent crossing is manifest. There is not even any marked tendency for the sub-optimal and supra-optimal graphs to slope downward to the right. Practically the only tendency toward any agreement is exhibited between the sub-optimal and supra-optimal graphs for the first nine cultures as arranged in figure 9. These two graphs appear, in this region, to rise and fall simultaneously, but the fifth culture (R1C4) of the supra-optimal series is omitted, so that even this amount of agreement is uncertain. It should be emphasized that the order in which the cultures are arranged for the graphs of figure 9, is not at all the same as their order in figure 5, so that these two sets of graphs

are not directly comparable excepting in the general way just pointed out. (For a direct comparison see figure 15.)

It therefore appears, that the physiological value, for the production of root yields, of any given set of salt proportions unquestionably varies as the total concentration of the medium is altered, which is quite similar to the general conclusion reached from the study of top yields.

Relation of yields of roots to the proportions of the chemical ions. The discussion of root yields with reference to the proportions of the three cations in the solutions will follow the same general lines as were followed in the

TABLE VIII

Minimum and maximum values for the three cation ratios, and ranges of these values, for each entire series and for high and low yields of wheat roots with each total concentration tested. Also, these ratio values for the three best solutions for yields of roots.

		Mg/Ca RATIO			Mg/K RATIO			Ca/K RATIO		
		Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)	Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)	Sub-optimal (0.1 atm.)	Optimal (1.75 atm.)	Supra-optimal (4.0 atm.)
Entire series	Minimum	0.24	0.24	0.24	0.18	0.18	0.18	0.09	0.09	0.09
	Maximum	15.40	15.40	18.80	11.10	11.10	13.78	5.76	5.76	6.40
	Range	15.16	15.16	18.56	10.92	10.92	13.60	5.67	5.67	6.31
Low yields	Minimum	0.24	0.32	7.52	0.25	0.21	8.18	0.46	0.22	0.44
	Maximum	2.06	2.21	18.80	6.37	3.56	13.78	5.76	3.59	1.46
	Range	1.82	1.89	11.28	6.12	3.35	5.60	5.30	3.37	1.02
High yields	Minimum	0.89	2.29	0.75	0.18	0.53	0.54	0.09	0.11	0.10
	Maximum	12.23	9.58	11.64	4.26	10.33	2.33	0.45	1.45	0.86
	Range	11.34	7.29	10.89	4.08	9.80	1.79	0.36	1.34	0.76
Highest yields		11.55	6.74	2.16	2.78	9.72	1.16	0.24	1.44	0.54

corresponding discussion of top yields, but it will be less detailed. The maximum and minimum ratio values for the regions of high and low root weights, as shown on the diagrams of figures 6, 7, and 8 are set forth in table VIII, which conforms in every way with table VII.

As in the case of the top yields, the areas of high and of low dry weights of roots are generally limited to certain ranges of the three cation ratio values here considered, these ranges being always less extensive than the corresponding total ranges. In two cases the limiting range of ratio values embraces almost all of the corresponding total range: (1) in the sub-optimal series the area of low root yields (fig. 6) embraces all but the very lowest

values of the ratio Ca/K, and (2) in the optimal series the area of high yields (fig. 7) embraces all but the very lowest and very highest values of the ratio Mg/K.

For all three total concentrations, the solutions giving high root yields are clearly defined as having very low values of the Ca/K ratio and rather extensive medium ranges of the ratios Mg/Ca and Mg/K. Further details may be discovered from a study of table VIII and of the diagrams of figures 6–8, but their statement here would add nothing leading to valuable generalizations at present. It is clear that the ratio values characterizing solutions giving low or high yields vary in a pronounced way with the alteration of the total concentration.

The atomic proportions of Mg, Ca, and K that characterize the three solutions giving the highest yields of roots in each series deserve special attention here, as in the case of top yields. For the sub-optimal total concentration (0.1 atm.) the most perfectly balanced solution for root yields contains 2.78 atoms of magnesium and 0.24 atoms of calcium for each single atom of potassium. For the optimal series (total concentration 1.75 atm.), these atomic proportions are Mg, 9.72: Ca, 1.44: K, 1.00, and for the supra-optimal series (total concentration 4.0 atm.), they are Mg, 1.16: Ca, 0.54: K, 1.00. The last of these sets of proportions is the only one of the three that is the same for the highest yields of both roots and tops. The cation atomic proportions characterizing the best physiological balance for root yields, as here brought out, vary as markedly and in as recondite a way, with variation in total concentration, as they do in the case of yields of tops.

3. APPARENT CONDITION OF PLANTS

Condition of tops

No apparent differences (aside from those of size) in the tops of the wheat plants of any series occurred during the first ten days of their growth, and none appeared at all in the sub-optimal series. In the optimal and supra-optimal concentrations, however, evidences of disturbed growth appeared in the tops of a number of cultures, usually about the tenth day after the young plants had been placed in the solutions. This disturbance was practically identical with that described by Tottingham and called by him magnesium injury. It manifested itself in two forms.

The more pronounced of these forms of injury consisted in a lateral rolling backward of the entire length of the injured leaves. Leaves so injured showed the effect at a very early stage and never attained the mature form and size. The young leaves, just emerging from the sheath, rolled back laterally throughout their entire length, frequently also coiling into a close spiral. The first few leaves produced by the plants usually escaped injury

altogether or suffered only from the less pronounced form to be described below, but the later leaves (in cultures where pronounced injury occurred) were attacked at a very early stage of their development, even while they were emerging from the sheath.

The pronounced form of injury did not occur on leaves that had already developed to the usual size, though such leaves were frequently affected by the less pronounced form. This form of injury manifested itself, in either young or old leaves that had previously appeared normal, by a yellowing and shrivelling of a small region several centimeters from the tip. The distal portion, above the first lesion, remained green and apparently in healthy condition for some time, but finally died. This less pronounced form of injury usually began with the third leaf formed, mainly after the leaf had attained a considerable size. It did not appear to retard growth perceptibly; indeed, the largest and most vigorous cultures, in both optimal and supra-optimal series, always showed this less pronounced form of leaf injury. Where both forms of injury occurred on the same plant, the less pronounced form was the first to make itself evident.

The cultures of the optimal and supra-optimal series may be divided, according to the injury they sustained, into three classes: (1) those that were without injury, (2) those that exhibited only the less pronounced form of injury, and (3) those that exhibited the more pronounced form. For the optimal total concentration of the solutions the observations on leaf injury, from both series A and B, are summarized in the triangular diagram of figure 10, and a similar presentation of these observations for the supra-optimal concentration of the solutions is given in the diagram of figure 11. In these diagrams the cultures suffering from the pronounced form of injury occupy the area denoted by crosses. These cultures were also affected by the less pronounced form of injury. Those exhibiting only the less pronounced form occupy the area denoted by small circles. The area representing uninjured cultures is unshaded. The three areas thus shown for each diagram are separated, as heretofore in similar cases, by broken lines.

For the optimal series, the area of slight injury (marked by small circles) occupies the entire left central portion of the triangle (fig. 10), extending from base to apex and reaching the left margin at culture R8C1. The area of severe injury (marked by crosses) lies along the left margin of the triangle, including all the cultures on this margin excepting R8C1, and extending to the right, at the lower left angle of the triangle, to include culture R1C2. On the supra-optimal triangle (fig. 11), the area of slight injury occupies a position corresponding to that of the same area on the optimal triangle. The area of severe injury in this series occupies the same region as in the optimal diagram, but extends farther to the right in its lower portion, so as to include cultures R1C2, R2C2, and R3C2.

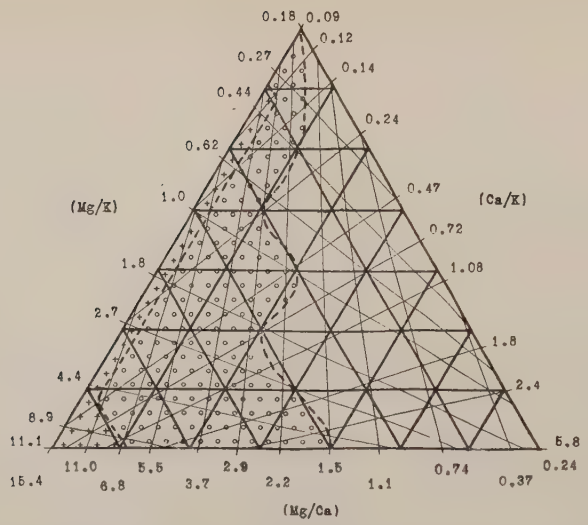

FIG. 10. Triangular diagram for optimal total concentration (1.75 atm.), showing the solutions producing no leaf injury (unshaded), those giving only slight leaf injury (indicated by small circles), and those giving severe leaf injury (indicated by crosses).

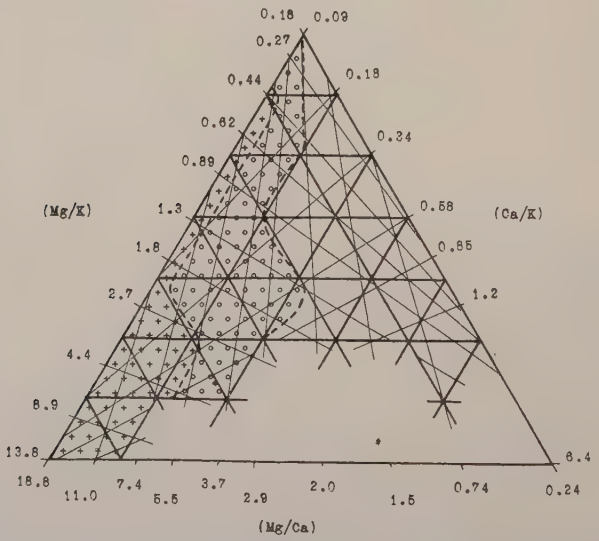

FIG. 11. Triangular diagram for supra-optimal total concentration (4.00 atm.) showing relation of salt proportions to leaf injury, as in figure 10.

A study of the diagrams of figures 10 and 11 brings out the fact that the severely injured cultures have osmotic partial concentrations of $Ca(NO_3)_2$ varying from 0.1 (R1C1) to 0.2 (R1C2), but culture R8C1, in which this concentration has also a value of 0.1, was not severely injured. It is thus clear that the partial osmotic concentration of $Ca(NO_3)_2$ is not a clearly limiting factor in the production of this injury. Similarly, the injured cultures have osmotic partial concentrations of $MgSO_4$ varying from 0.2 (R7C1) to 0.8 (R1C1), while culture R8C1, not seriously injured, exhibits this partial concentration as 0.1. From this it appears that an osmotic partial concentration of $MgSO_4$ as low as 0.1 does not produce severe injury. Nevertheless, it is clear that values of this partial concentration from 0.2 to 0.6 may or may not be severely injurious, according to other conditions. Finally, the osmotic partial concentration of KH_2PO_4 may have any value from 0.1 to 0.7 without producing severe leaf injury, and also, for the same range, it may produce injury. The only value of this partial concentration not ever accompanied by pronounced injury is 0.8 (R8C1). From these considerations it may be concluded that severe injury is definitely absent only when the osmotic partial concentration of $Ca(NO_3)_2$ is higher than 0.2, when that of $MgSO_4$ is lower than 0.2, and when that of KH_2PO_4 is higher than 0.7. It is thus obvious that the conditions determining severe injury must be related to the relative proportions of the three salts rather than to osmotic partial concentration of any one salt, a conclusion already reached by Tottingham for his similar series of cultures.

Considering the ratios of the osmotic partial concentrations, as was done by Tottingham, it appears that severe injury accompanies the ratio $MgSO_4/Ca(NO_3)_2$ when this ratio has a value between 2.0 (R7C1) and 8.0 R1C1. For the remainder of the series, not severely injured the value of this ratio varies from 1.0 (R8C1, R6C2) to 3.0 (R2C2, optimal). This makes it clear that no severe injury is produced with these ratio values below 2,0, and that severe injury always occurs when these values are greater than 3.0. Osmotic ratio values of $MgSO_4/Ca(NO_3)_2$ from 2.0 to 3.0 are thus questionable, and may or may not produce severe injury, apparently according to other conditions. The highest value of this ratio with which no injury occurred is 1.33 (culture R3C4). If therefore seems that no injury is to be expected, in 3-salt solutions such as were here employed, with osmotic ratios of $MgSO_4/Ca\ (NO_3)_2$ whose values are less than 1.33. Tottingham (page 203) has placed the limiting value of this ratio at 0.25, and notes that osmotic ratios of $MgSO_4/Ca(NO_3)_2$ with values of 2.0 or above may be expected to produce marked injury in his 4-salt solution.

A consideration of the cation ratio values with reference to leaf injury brings out some interesting features. The ranges of injury indicated on the diagrams of figures 10 and 11 are seen at once to bear no definite relation to either of the ratios Mg/K or Ca/K; these regions embrace all or nearly

all of the total ranges of the values of both these ratios. On the other hand, it is at once obvious that solutions characterized by values of the ratio Mg/Ca below 1.5 give plants without injury in the optimal series, and those where this ratio value is below 2.2 give uninjured plants in the supra-optimal series. From these considerations it appears that the limit of slight injury is practically set by the magnitude of the ratio of magnesium to calcium. The limit of severe injury is not so readily defined; it surely is related to other properties of the solution than the Mg/Ca ratio.

Condition of roots

No great differences between the roots of the various cultures of the sub-optimal series were apparent. The roots of the optimal and supra-optimal series, however, showed marked differences even during the first ten days of their growth. During the first twelve days after they were placed in the nutrient solutions, the roots of cultures R1C1, R1C2, R2C1, R3C1, R4C1, R5C1, R6C1, and R7C1, were distinguished from the remaining cultures of these series by the absence of secondary roots and by short, thickened primary roots. During the later stages of growth numerous lateral roots appeared in these cultures, but took the form of short, stubby outgrowths. In cultures R1C1, R2C1, R3C1, and R4C1, these numerous lateral roots assumed the form of small, rounded tubercles. This latter condition of the roots was coincident with the most severe injury to the leaves, and injured roots were confined to the areas of severe leaf injury on the diagrams of figures 10 and 11. The root systems of cultures characterized by slight leaf injury appeared to be particularly *well* developed, although the lateral roots of cultures R1C3 and R2C2 were somewhat shorter than those of the other cultures with slight leaf injury. In cultures where leaf injury was not apparent at all, root development did not appear to be so vigorous, in general, as in those suffering slight leaf injury. It thus appears that the most vigorous root growth (for optimal and supra-optimal total concentrations) may be expected to occur in solutions whose osmotic ratio $MgSO_4/Ca(NO_3)_2$ is somewhat above 1.33. The partial concentration of KH_2PO_4 appears to have no influence upon the plants, as far as either leaf or root injury is concerned.

4. TRANSPIRATION DATA

Transpiration as a measure of growth

Introductory. Transpiration being a process that is going on at all times in the living plant, one to which many other plant processes are surely related, and also one that is somewhat readily measured, it has seemed worth while to study the relative amounts of water lost from the various cultures during their growth and to compare these transpiration data with the results of the other plant measurements.

The relative rate of water loss has been emphasized by several writers as an approximate measure of plant growth. Thus Whitney and Cameron[22] and other workers with plant cultures in the U. S. Bureau of Soils,[23] have taken the total amount of transpirational water loss during the growth of a culture as being more or less directly proportional to the growth of the plant. The relation between the amount of transpiration, dry weight, leaf surface, etc., for cultures of wheat during the first few weeks of their growth, was studied by Livingston,[24] who came to the conclusion that in many instances the amount of water lost by plants of the same species and of the same age, grown in the same locality but in different soils or solutions, is roughly proportional to the extent of leaf surface, and therefore, to the size of the plants. Of course such a relation can be expected to hold only where the relative amounts of water lost by transpiration are determined only by the size of the plants, not by internal physiological conditions. If the plants differ internally in some manner that affects transpiration otherwise than by differences in size, then transpiration should not be a measure of the size, although it might still be a valuable indicator of the general health of the plants. The general complexity of the problem thus suggested, as to whether transpiration may be reasonably employed to indicate relative growth and health of plants, apparently furnishes the explanation for Harris's[25] unexplained remark that Livingston's data do not justify his conclusions in this regard.

The transpiration diagrams. As has been remarked, the amount of water lost from each culture during the period of its growth was determined by summing the various losses recorded during that period. The total loss thus obtained for each culture was then expressed in terms of the total loss for culture R1C1 of the same series, considered as unity. The relative loss thus obtained for each culture of series A and that for the corresponding culture of series B, were averaged in all cases.

Table IX presents the transpiration data in three sections, each section referring to a single total concentration of the medium. The first column of the table gives, as heretofore, the culture or solution numbers referring to the triangular diagrams. In each of the three sections of the table (sub-optimal, optimal, and supra-optimal), the first two columns give the losses, relative to the loss from culture R1C1 in each case, for series A and B, respectively. The third column of each section gives the average losses for series A and B together, also relative to the average loss for culture R1C1.

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[22] Whitney, M. and Cameron, F. K., Investigations in soil fertility. U. S. Dept. Agric. Bur. Soils Bull. 23. 1904.

[23] Livingston, B. E., Britton, J. C., and Reid, F. R., Studies on the properties of an unproductive soil. U. S. Dept. Agric. Bur. Soils Bull. 28. 1905.

Livingston, B. E., Further studies on the properties of unproductive soils. U. S. Dept. Agric. Bur. Soils Bull. 36. 1907.

[24] Livingston, B. E., Relation of transpiration to growth in wheat. Bot. Gaz. **40**: 178–195. 1905.

[25] Harris, F. S., Effects of variations in moisture content on certain properties of a soil and on the growth of wheat. Cornell Univ. Agr. Exp. Sta. Bull. 352. 1914.

TABLE IX

Transpiration data for wheat grown 23 days in 3-salt solutions; series A, conducted from September 8 to October 1, series B, from November 13 to December 6, 1914.

CULTURE NUMBER	SUB-OPTIMAL TOTAL CONCENTRATION (0.1 ATM.)			OPTIMAL TOTAL CONCENTRATION (1.75 ATM.)			SUPRA-OPTIMAL TOTAL CONCENTRATION (4.0 ATM.)		
	Series A	Series B	Average	Series A	Series B	Average	Series A	Series B	Average
R1C1	1.00* (131)	1.00 (160)	1.00L (145)	1.00 (170)	1.00 (213)	1.00L (192)	1.00 (126)	1.00 (135)	1.00L (131)
C2	1.42	1.21	1.32	1.21	1.08	1.15	1.08	1.16	1.12
C3	1.41	1.41	1.41	1.17	1.12	1.15	.....	.....	.....
C4	1.56	1.55	1.56	1.16	1.19	1.18	.....	.....	.....
C5	1.78	1.27	1.53	1.19	1.14	1.17	.....	.....	.....
C6	1.91	1.57	1.74H	1.20	1.07	1.14	.....	.....	.....
C7	1.61	1.47	1.54	1.18	1.14	1.16	.....	.....	.....
C8	1.78	1.44	1.61H	1.15	1.14	1.15	1.06	1.35	1.21
R2C1	1.22	1.16	1.19L	1.07	1.08	1.08	0.97	1.07	1.02L
C2	1.38	1.35	1.37	1.14	1.11	1.13	1.11	1.16	1.14
C3	1.58	1.49	1.54	1.21	1.09	1.15	1.07	1.40	1.24H
C4	1.79	1.51	1.65H	1.15	1.08	1.12	.....	.....	.....
C5	1.59	1.58	1.59H	1.02	1.13	1.08	.....	.....	.....
C6	1.57	1.66	1.61H	1.15	1.17	1.16	1.15	1.33	1.24H
C7	1.91	1.46	1.69H	1.12	1.08	1.10	.....	.....	.....
R3C1	1.48	1.18	1.33	1.17	0.99	1.08L	0.86	1.15	1.01L
C2	1.69	1.50	1.60H	1.31	1.09	1.20H	1.09	1.27	1.18
C3	1.66	1.54	1.60H	1.35	1.19	1.27H	1.15	1.36	1.26H
C4	1.86	1.67	1.77H	1.14	1.15	1.15	1.14	1.27	1.21
C5	1.78	1.51	1.65H	1.16	1.14	1.15	1.13	1.27	1.20
C6	1.80	1.64	1.72H	1.15	1.16	1.16	1.15	1.31	1.23H
R4C1	1.36	1.19	1.28	1.15	1.07	1.11	1.06	1.16	1.11
C2	1.74	1.34	1.54	1.21	1.08	1.15	1.08	1.31	1.20
C3	1.75	1.48	1.62H	1.18	1.09	1.14	1.23	1.38	1.31H
C4	1.66	1.50	1.58H	1.24	1.09	1.17	1.15	1.34	1.25H
C5	1.86	1.59	1.73H	1.24	1.27	1.26H	1.22	1.34	1.28H
R5C1	1.37	1.19	1.28	1.14	1.16	1.15	1.00	1.13	1.07L
C2	1.58	1.36	1.47	1.34	1.20	1.27H	1.14	1.30	1.22
C3	1.66	1.37	1.52	1.24	1.14	1.19H	1.07	1.36	1.17
C4	1.53	1.34	1.44	1.28	1.06	1.17	1.19	1.26	1.23H
R6C1	1.45	1.20	1.33	1.23	1.13	1.18	1.05	1.18	1.12
C2	1.70	1.38	1.54	1.21	1.13	1.17	1.05	1.24	1.15
C3	1.74	1.44	1.59H	1.23	1.08	1.16	1.05	1.22	1.14
R7C1	1.50	1.21	1.36	1.19	1.07	1.13	0.98	1.10	1.04L
C2	1.71	1.38	1.55	1.28	1.21	1.25H	1.03	1.16	1.10
R8C1	1.47	1.17	1.32	1.24	1.00	1.12	1.09	0.96	1.03L
K**	1.84	1.57	1.71	1.16	1.07	1.12	0.99	1.04	1.02
T**	1.54	1.51	1.53	1.23	1.22	1.23	1.18	1.19	1.19

* The loss for culture R1C1 is always taken as unity, and the other losses are expressed in terms of this. The actual loss for culture R1C1 is given in parenthesis, in each case, in cubic centimeters.

** K and T represent Knop's solution and Tottingham's best solution, respectively: these data are introduced for comparison.

The letters L and H, following the average data as in the tables III, IV and V, represent numbers lying, respectively, within the lower and within the upper one-fourth of the total range of the series of averages.

The average data of table IX were plotted on the triangular diagrams, as were those of the dry weight yields, and the diagrams thus obtained were compared with the yield diagrams already given (figs. 2–4 and 6–8). Since the notations L and H of table IX indicate the low and high regions of these transpiration diagrams, the latter need not be here presented. The following observations obtained by comparing them with the corresponding yield diagrams may be given, however.

On the sub-optimal diagram the region of low transpiration embraces only the extreme lower portion (culture R1C1 and R2C1) of the region of low yields of tops (fig. 2). The region of high top yields lies entirely within that of high transpiration, but the latter region is considerably larger than the former. These two diagrams agree, in general, in showing the lower top yields and lower transpirations as occupying the left side of the triangle, while the higher yields and transpirations occupy the middle and lower right. About as good agreement is manifest between the diagrams of root yields (fig. 6) and that of transpiration, in the sub-optimal series. It is to be emphasized here, however, that *low* transpiration corresponds to *high* yields of roots, while *high* transpiration corresponds to *low* yields of roots.

In the optimal series, there is an exceedingly close agreement between transpiration and yield of tops (fig. 3), both for the regions of low and for those of high values. Here the amount of water transpired during the growth of the plants appears to be as good a criterion as is the final dry weight, for judging the comparative growth obtained in the different solutions. Comparison of the transpiration diagram with that of root yields for the optimal series (fig. 7), shows that there is here no detailed agreement. All that may be said is that the *low* transpiration data agree, in a general way, with the data of *high* root yields, by lying to the left of the region of *high* transpiration and and of *low* root yields.

The supra-optimal diagram of transpiration agrees very closely, but not quite exactly, with the diagram of top yields (fig. 4); the agreement is exact in the case of the regions of low values. No general agreement is to be noted between the diagram of transpiration and that of root yields (fig. 8) in the supra-optimal series, though the culture giving highest root yields also gave highest transpiration.

From the last three paragraphs it appears that the amount of water lost by the plants is generally a valuable indication of the top yields, under the conditions of these cultures, low transpiration corresponding to low yield of tops and high transpiration to high yield. This is especially true of the optimal and supra-optimal total concentrations. It also appears that there is no marked correlation between yield of roots and transpiration, though the

sub-optimal and optimal series agree in showing a general, but inverse, correspondence in this regard. For the sub-optimal series it appears that *high* transpiration is correlated with low root yields.

Relation of transpiration to total concentration of the medium. To bring out the relations between the amounts of water lost by transpiration and the total concentration of the nutrient solution, graphs of the average transpiration data for each of the three series were prepared, in a manner quite similar to that employed for the study of top and root yields (figs. 5 and 9). These three transpiration graphs are shown in figure 12. The actual losses for the optimal series are here arranged in the order of their magnitudes, from the highest to the lowest, and are then plotted to form the nearly straight line of the figure. With the various cultures arranged in the order

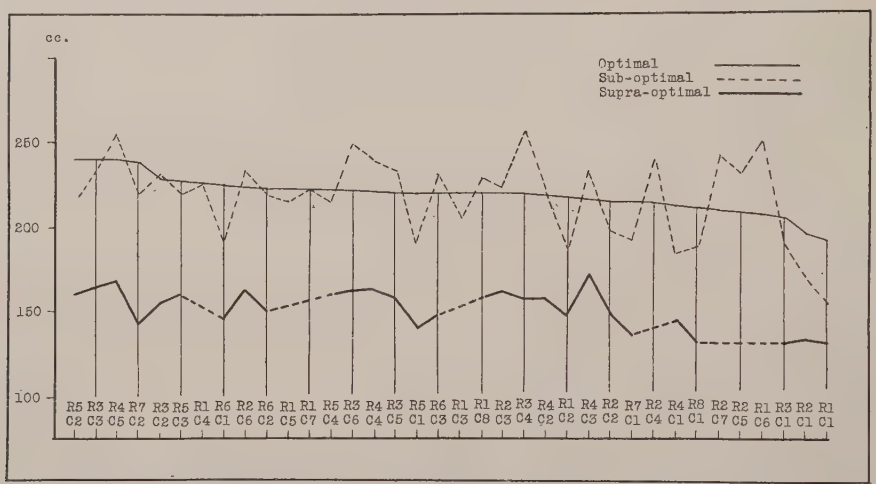
cc.
Optimal
Sub-optimal
Supra-optimal
250
200
150
100
R5 R3 R4 R7 R3 R5 R1 R6 R2 R6 R1 R1 R5 R3 R4 R3 R5 R6 R1 R1 R2 R3 R4 R1 R4 R2 R7 R2 R4 R8 R2 R2 R1 R3 R2 R1
C2 C3 C5 C2 C2 C3 C4 C1 C6 C2 C5 C7 C4 C6 C4 C5 C1 C3 C3 C8 C3 C4 C2 C2 C3 C2 C1 C4 C1 C1 C7 C5 C6 C1 C1 C1

FIG. 12. Amounts of water lost by transpiration (cubic centimeters) from wheat plants grown with sub-optimal, optimal, and supra-optimal total concentrations.

determined by this graph the two other series are plotted on the same scale. These three graphs show clearly that there is no general tendency for transpiration to be either higher or lower with the sub-optimal than with the optimal total concentration. On the other hand, it is plain that none of the transpiration data for the supra-optimal series is nearly as great as are the corresponding data for the sub-optimal and optimal series. This latter relation was brought out in the study of the relation of top yields to total concentration (fig. 5), but in that case a pronounced and general difference is observed between the top yields of the sub-optimal and optimal series. Since no such difference is here manifest, it is clear that the criterion of transpiration, while valuable as indicating large differences in growth (without the destruction of the plants), is not always as definite in its indications as is the criterion of dry weight of tops.

Water requirement

Introductory. The relations between the amounts of water lost by transpiration and the dry weight yields of the various cultures may be studied by means of the ratios of transpiration to yield. Such ratios represent the water requirements of the plants, being the amount of water required, in each case, to produce a single gram of yield.

Apparently the first worker to give attention to water-requirement as a measurable physiological character of plants was Woodward,[26] whose work was carried out over 215 years ago. This author found that plants grown in water with low salt content had a much higher water requirement (per unit of *green* weight) than those grown in water containing more dissolved salt. Many other experimenters have studied the water requirements of plants grown under various conditions, although water cultures have been employed in but little of this work. Physiologists do not seem generally to have realized the importance of this criterion of plant growth, and most of the experiments reviewed in Briggs and Schantz's[27] excellent and exceedingly useful summary of the literature of this subject were carried out by agriculturists, and with only approximate control of the various effective conditions. Sorauer's experiments with water cultures may, however, be mentioned here, and also those of Heinrich.

Sorauer[28] studied rye, barley, wheat and oats, grown 53 days in "normal" ([1885], page 87) nutrient solutions of different total concentrations (from 0.05 to 1.00 "per cent") and found that the water requirement (per unit of dry yield) decreased with increase in the total concentration of the medium. Thus, according to Briggs and Schantz's ([1913], page 55) computations of Sorauer's results, the water requirement for wheat in these tests was 768 ± 40 when the total concentration of the solution was 0.05 per cent, and only 469 ± 18 when the total concentration was 0.50 per cent.

Heinrich[29] grew oats to maturity in nutrient solutions containing $4H_2KPO_4 + CaCl_2 + 5Ca(NO_3)_2 + 2MgSO_4 + 2Fe$ (Briggs and Schantz [1913], page 55), with total concentrations varying from 0.1 g. to 3.0 g. per liter. The weakest solution showed a water-requirement (per unit of dry yield) of 642 and the next to the weakest (0.25 g. per liter) gave a corresponding value of 688. Throughout the remainder of the series the water-requirement decreased as the total concentration of the medium increased, and the value obtained for the plants grown in the solution containing 3.0 g. per liter was 515. Thus,

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[26] Woodward, J., Some thoughts and experiments concerning vegetation. Phil. Trans. Roy. Soc. London **21**: 193–227. 1699.

[27] Briggs, L. J., and Shantz, H. L., The water requirement of plants. II. A review of the literature. U. S. Dept. Agric. Bur. Plant Ind. Bull. 285. 1913.

[28] Sorauer, P., Nachtrag zu den "Studien über Verdunstung." Forsch. Geb. Agric. Phys. **6**: 79–96. 1883.

[29] Heinrich, R., Ueber die Wassermengen, welche die Haferpflanze aus verschiedenen Nährstoff-Concentrationen während ihrer Vegetationszeit verbraucht. Zweiter Bericht über die Verhältnisse und Wirksamkeit der Landwirtschaftlichen Versuchs-Station, Rostock. Pages 179–174. 1894.

with the exception of the very weakest solutions (where the plants were obviously unhealthy), the water requirement is less with more concentrated solutions and greater with weaker ones, which is in general agreement with the conclusion reached by Sorauer.

In the present case the average amount of water lost by transpiration from each culture in series A and B was divided by the corresponding yield of tops and also by the corresponding yield of roots. The water requirement ratios thus obtained, for tops and for roots, expressed in terms of the corresponding ratio for culture R1C1, are set forth in table X. The actual average water requirements (grams of water required to produce a single gram of dry material) are given for culture R1C1, in each case, this number being placed in parenthesis below the relative value (unity) of culture R1C1 in the comparative series. The letters L and H indicate, as in previous tables, that the numbers opposite which they are placed fall within the lower one-fourth and within the upper one-fourth, respectively, of the total range of their respective series.

Relative water requirements. A study of the six triangular diagrams prepared from the data of table X brings out several interesting suggestions, but no precise generalizations can be made in this connection, and the diagrams will not be given here. It may, however, be worthy of mention that, in the optimal series, low water requirement of tops corresponds, in a general way, with high top yield, while in the sub-optimal series low water requirement of roots corresponds with low top yield. These diagrams emphasize the fact that optimum physiological balance, or the best salt proportions, of the nutrient medium, to give either low or high water requirement ratios, does not occur in the same solutions in the three different series. How a given set of salt proportions affects the plant in this respect is determined by the total concentration of the mixture.

Relation of total concentration to the actual magnitudes of the water requirement ratios. As in the cases of yields of tops and roots and of transpiration (figs. 5, 9 and 12), the actual water requirements of tops and of roots have been graphically represented in a linear way, and these graphs are given in figures 13 and 14. In both cases the data for the optimal series were arranged in a decreasing order and then plotted as ordinates, with arbitrary, equal abscissa increments representing the different solutions. The order of the solutions or cultures is thus not the same in figures 13 and 14. After this order was determined as the descending series for the optimal concentration, the corresponding data for the sub-optimal and supra-optimal concentrations were plotted on the same chart, in each case. These charts bring out the general relations between total concentration and water requirements of tops and of roots.

a. Water requirement of tops. For the water requirement of tops (fig. 13) it is seen at once that the total concentration of the medium determines the

TABLE X

Amount of water required for the production of each gram of yield of tops and of roots (water requirement), relative to that of culture R1C1. The data are averages from series A and B.

CULTURE NUMBER	SUB-OPTIMAL TOTAL CONCENTRATION (0.1 ATM.)		OPTIMAL TOTAL CONCENTRATION (1.75 ATM.)		SUPRA-OPTIMAL TOTAL CONCENTRATION (4.0 ATM.)	
	Tops	Roots	Tops	Roots	Tops	Roots
R1C1	1.00L*	1.00L	1.00	1.00L	1.00L	1.00
	(559)	(1407)	(466)	(1802)	(363)	(1506)
C2	1.08L	1.23L	0.96	1.03L	1.00L	1.09H
C3	1.13	1.34	0.95	1.22	.....	.....
C4	1.20	1.71	1.02H	1.10	.....	.....
C5	1.20	1.74	0.92L	1.17	.....	.....
C6	1.25H	1.76	0.94	1.15	.....	.....
C7	1.23H(?)	1.98H	1.06H	1.15	.....	.....
C8	1.28H	1.99H	0.99	1.21	1.07	1.11H
R2C1	1.16	1.00L	1.00	1.07L	1.05	0.93
C2	1.10	1.31	1.00	1.07L	1.00L	1.01
C3	1.11	1.65	0.92L	1.24H	0.97L	1.05H
C4	1.11	1.76	0.89L	1.18	.....	.....
C5	1.13	2.07H	0.91L	1.21	.....	.....
C6	1.12	2.13H	0.96	1.19	0.96L	1.05H
C7	1.22	2.09H	0.91L	1.07L	.....	.....
R3C1	1.21	0.95L	0.93L	1.06L	0.96L	0.92
C2	1.24H	1.34	0.96	1.12	1.05	1.02
C3	1.13	1.51	0.93L	1.18	1.00L	1.07H
C4	1.12	1.86H	0.90L	1.21	0.97L	1.10H
C5	1.06L	1.94H	0.92L	1.25H	0.96L	1.02
C6	1.31H	1.90H	1.00	1.25H	1.10H	1.00
R4C1	1.28H	0.97L	0.99	1.07L	1.04	0.87L
C2	1.26H	1.24L	0.90L	1.05L	0.97L	0.92
C3	1.13	1.53	0.90L	1.25H	0.95L	0.98
C4	1.05L	1.85H	0.91L	1.29H	1.02	0.98
C5	1.06L	1.97H	0.98	1.21	1.02	1.03
R5C1	1.21	1.00L	0.96	1.08L	1.08H	0.84L
C2	1.03L	1.26	0.91L	1.18	1.01	0.99
C3	1.08L	1.69	0.96	1.29H	1.00L	1.07H
C4	1.12	2.05H	0.92L	1.14	1.02	1.00
R6C1	1.22	1.01L	1.01	1.11	1.07	0.87L
C2	1.03L	1.41	0.99	1.25H	0.98L	0.94
C3	1.11	1.64	0.96	1.32H	1.05	1.01
R7C1	1.26H	0.98L	0.98	1.10	1.03	0.84L
C2	1.18	1.18	0.95	1.23	1.05	0.90L
R8C1	1.19	0.96L	1.03H	1.10	1.13H	0.86L
K**	1.29	1.94	1.02	1.18	0.98	1.02
T**	1.02	1.66	0.96	1.20	0.97	0.95

* The water requirement for culture R1C1 is always taken as unity, and the other water requirements are expressed in terms of this. The actual water requirement for culture R1C1 is given in parenthesis, in each case.

** K and T represent Knop's solution and Tottingham's best solution respectively; these are introduced for comparison.

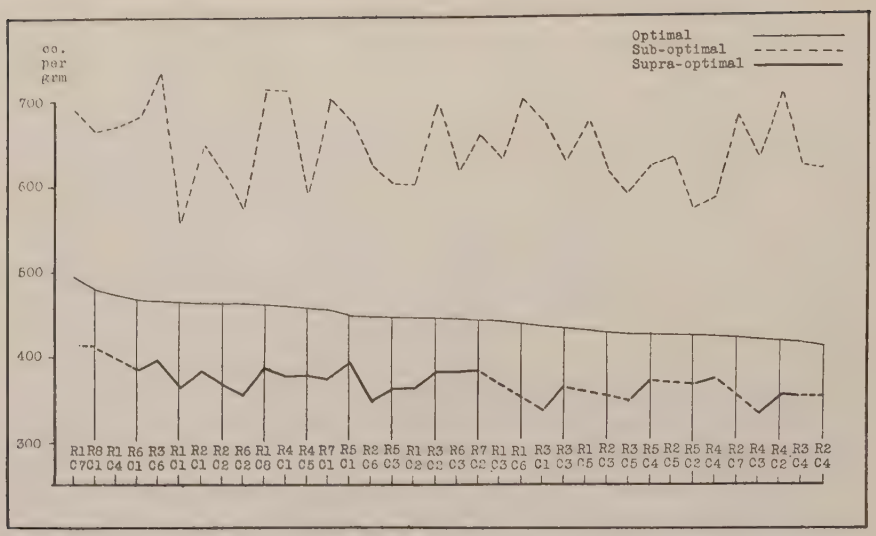

FIG. 13. Water requirement (cubic centimeters) per gram of wheat tops grown in sub-optimal, optimal, and supra-optimal total concentrations.

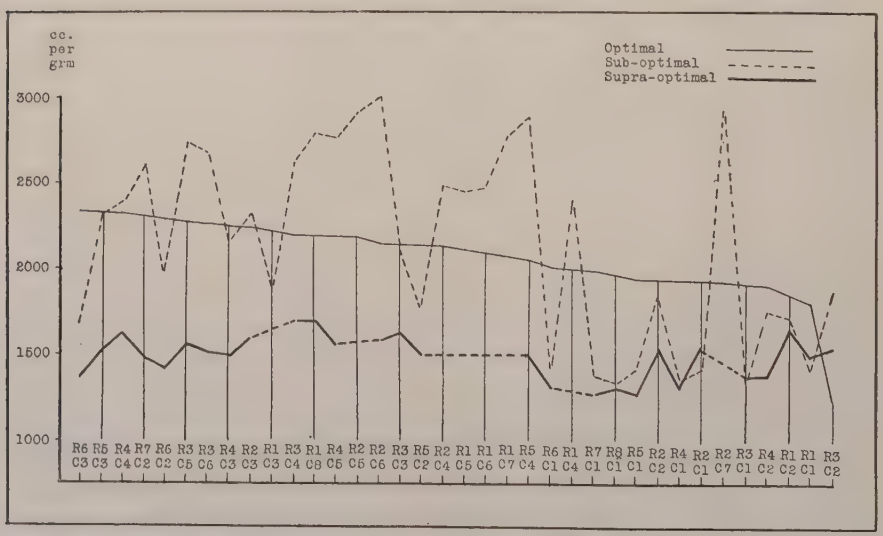

FIG. 14. Water requirement (cubic centimeters) per gram of wheat roots grown in sub-optimal, optimal, and supra-optimal total concentrations.

general position of the graph. There is here no crossing of the graphs; the highest water requirements of tops are all shown as occurring in the sub-optimal series, the lowest requirements are those of the supra-optimal series, and the optimal series exhibits water requirements of tops that occupy an intermediate position. A clear generalization is here indicated: the higher the total concentration the lower is the amount of water required for the production of a gram of dry tops. This conclusion is perfectly definite, for the conditions of the present study at least, and appears to agree with what might be expected from an *a priori* consideration of the problem in hand. It appears that water loss by transpiration is retarded more by high concentration of the nutrient medium than is the production of yield of tops, and it seems quite clear that this is due to a physical (rather than to a chemical) property of the solution, being probably related directly to osmotic phenomena. With more concentrated solutions the resistance to water absorption by the roots is increased, and this resistance, in turn, decreases the transpiring power[30] of the plants.

The arrangement of these three graphs of water requirements of tops is entirely different from that of the graphs of dry weights of tops (fig. 5). The optimal total concentration gives highest yields of tops and medium water requirements of tops, the supra-optimal concentration gives medium yields of tops and lowest water requirements, and the sub-optimal concentration gives lowest yields and highest water requirements. It appears that a very important generalization (as far as the water relations of plants are concerned) is here touched upon, one that will surely repay more thorough study.

b. Water requirement of roots. The graphs of figure 14 indicate that there is no clear relation between water requirement of roots and total concentration of the medium, for the sub-optimal and optimal total concentrations. On the other hand, these graphs do show a very clear relation, as to the water requirements of roots, between the optimal and supra-optimal total concentrations. The root water requirement is almost always markedly lower, for any set of salt proportions, in the supra-optimal solutions than in the optimal ones. The relations are here about the same as for the water requirements of tops, as far as these two higher total concentrations are concerned, and the same condition holds in comparison with transpiration (fig. 12). In a general way it may be said that the root water requirements for the sub-optimal concentration are lower and more nearly like those for the optimal concentration than is the case with the water requirements of tops.

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[30] Livingston, B. E., and Hawkins, Lon. A., The water-relation between plant and soil. Carnegie Inst. Wash. Pub. **204**: 3–48. 1915.

Pulling, H. E., and Livingston, B. E., The water-supplying power of the soil as indicated by osmometers. Carnegie Inst. Wash. Pub. **204**: 49–84. 1915.

Comparison of figures 5, 12, 13 and 14, shows that the relation between the optimal and supra-optimal total concentrations is much the same, whether this relation is judged by the criterion of dry weight of tops, by that of transpiration, by that of water requirement of tops, or by that of water requirement of roots.

5. GENERAL COMPARISON OF QUANTITATIVE PLANT DATA

Relation between the areas of low, medium, and high relative plant values, as shown on the various triangular diagrams

The quantitative plant data that have been presented in the preceding sections (those of yield of tops, yield of roots, transpiration, water requirement of tops and water requirement of roots) have been studied with reference to their distribution into areas of low, medium, and high values on the triangular diagrams. A range of total concentration—the physical property of the nutrient medium—from 0.1 atmosphere to 4.0 atmospheres has been studied, this total range being represented in the experiments by the limiting concentrations just mentioned and by an optimal concentration of 1.75 atmospheres. For each kind of plant measurement three triangular diagrams have thus been required, each diagram corresponding to one of these three total concentrations. The chemical character of the nutrient medium,—the proportions of the three main component salts,—has been studied by varying the salt proportions, in each of the three total concentrations, from osmotic proportions of 1 : 1 : 8 to those of 1 : 8 : 1 and to those of 8 : 1 : 1, the increments of variation being always one-tenth of the total diffusion tension or possible osmotic pressure of the solution as a whole. The total range of salt proportions has thus been represented by 36 different sets of proportions in each case, each set of proportions having its particular location on the triangular diagram. The position of a given solution on the diagram thus characterizes it as having a definite set of salt proportions (ion ratio values, etc.), or as having a certain complex of *chemical* properties, and the particular one of the three diagrams on which a given solution is located characterizes it as having a certain *physical* character determined by its total concentration.

It is of course clear that salt proportions other than those actually employed might have been tested, and that each of these would have had a definite location on the triangle. It is also obvious that total concentrations other than the three here employed might have been included in the experiments, and each one of these would have called for a separate triangle of its own. The whole system of possible variations in the chemical and physical properties of the nutrient solutions here dealt with may be pictured by means of a solid diagram, a right prism with an equilateral triangle as base. Passing from below upward, each successive horizontal (triangular) section of this

prism may represent a different total concentration of the nutrient solution, and each vertical line passing through the prism (thus cutting all the horizontal triangular sections) may represent a different set of salt proportions.

The various average values obtained for the five different plant measurements considered have been studied by plotting them on their respective diagrams, always expressing each value in terms of that for solution R1C1 of the same diagram, and the area of each diagram has been separated into three portions, designated as the areas of low, medium, and high values. Values of any plant measurement that lie within the lower one-fourth of the total range of that particular measurement, for that particular total concentration, have been termed low values; those lying within the upper one-fourth have been termed high values; and all other values for that kind of measurement and for that total concentration have been termed medium values. This notation simplifies the problem of comparing a large number of measurements, and the grouping of the thirty-six different values into but three classes should tend to avoid many complications arising from smaller variations in the values, brought about by the influence of unknown conditions upon the growth and development of the plants.

To compare all the different plant measurements and to relate them to the chemical and physical conditions of the solutions in which the plants were grown presents a somewhat complicated problem, which has been attacked only in part in the foregoing discussions. For each kind of plant measurement it is necessary to determine how the value alters with its position on the triangle and also how it alters with the position of the triangle in the prismatic diagram. The sub-optimal diagram of these studies may be considered as the lower base of the prism in question, the supra-optimal triangle being the upper base, while the optimal triangle is a horizontal section of the prism between the two bases. Each kind of plant measurement requires a prism of its own and a not unimportant part of the interpretation of the results involves comparisons between similar areas or points in the different prismatic diagrams.

Some of these various and complicated relations have been brought out in the foregoing discussions and still others will be evident from the tabular summary of all quantitative plant measurements presented in table XI. This table shows the relative value (low, medium, or high, denoted by the letters L, M and H) of each average plant measurement (series A and B combined) for each of the three different total concentrations and for each of the thirty-six different sets of salt proportions. The salt proportions are denoted by the solution numbers, in the first column, and the total concentrations are shown by the words sub-optimal, optimal, and supra-optimal, as heretofore. Table XI is virtually a summary of all the triangular diagrams, and of the columns of averages given in tables III, IV, V, IX, and X, in terms of low, medium and high values. From it may be determined the relations

TABLE XI

Summary of growth measurements of plants grown in 3-salt solutions of 36 different sets of salt proportions and of three different total concentrations, in terms of low (L), medium (M), and high (H) values, from tables III, IV, V, IX, and X.

	TOP YIELDS			ROOT YIELDS			TRANSPIRATION			WATER REQUIREMENTS					
										Tops			Roots		
Sol. No.	Sub-optimal	Optimal	Supra optimal	Sub-optimal	Optimal	Supra optimal	Sub-optimal	Optimal	Supra optimal	Sub-optimal	Optimal	Supra optimal	Sub-optimal	Optimal	Supra optimal
R1C1	L	L	L	M	M	L	L	L	L	L	M	L	L	L	M
C2	M	M	M	M	H	L	M	M	M	L	M	L	L	L	H
C3	M	M	—	M	L	—	M	M	—	M	M	—	M	M	—
C4	M	M	—	M	H	—	M	M	—	M	H	—	M	M	—
C5	M	M	—	L	M	—	M	M	—	M	L	—	M	M	—
C6	M	M	—	L	M	—	H	M	—	H	M	—	M	M	—
C7	M	M	—	L	M	—	M	M	—	H	H	—	H	M	—
C8	M	M	M	L	M	M	H	M	M	H	M	M	H	M	H
R2C1	L	L	L	M	M	M	L	M	L	M	M	M	L	L	M
C2	M	M	M	M	M	M	M	M	M	M	M	L	M	L	M
C3	M	M	H	M	L	M	M	M	H	M	L	L	M	H	H
C4	M	M	—	M	M	—	H	M	—	M	L	—	M	M	—
C5	M	M	—	L	L	—	H	M	—	M	L	—	H	M	—
C6	M	M	H	L	M	M	H	M	H	M	M	L	H	M	H
C7	M	M	—	L	M	—	H	M	—	M	L	—	H	L	—
R3C1	L	M	M	H	M	M	M	L	L	M	L	L	L	L	M
C2	M	M	M	M	H	M	H	M	M	H	M	M	M	M	M
C3	M	H	H	M	H	M	H	H	H	M	L	L	M	M	H
C4	H	M	M	M	M	M	H	M	M	M	L	L	H	M	H
C5	H	M	H	L	L	M	H	M	M	L	L	L	H	H	M
C6	M	M	M	M	L	M	H	M	H	H	M	H	H	H	M
R4C1	L	M	M	H	M	H	M	M	M	H	M	M	L	L	L
C2	M	M	M	H	H	H	M	M	M	H	L	L	L	L	M
C3	M	M	H	M	L	H	H	M	H	M	L	L	M	H	M
C4	H	M	M	L	L	H	H	M	H	L	L	M	H	H	M
C5	H	H	M	L	M	M	H	H	H	L	M	M	H	M	M
R5C1	L	M	L	H	H	H	M	M	L	M	M	H	L	L	L
C2	M	H	M	M	H	M	M	H	M	L	L	M	M	M	M
C3	M	M	M	M	L	M	M	H	M	L	M	L	M	H	H
C4	M	M	M	L	M	M	M	M	H	M	L	M	H	M	M
R6C1	L	M	M	H	H	H	M	M	M	M	M	M	L	M	L
C2	M	M	M	M	L	M	M	M	M	L	M	L	M	H	M
C3	M	M	M	M	L	M	H	M	M	M	M	M	M	H	M
R7C1	L	M	L	H	M	M	M	M	L	H	M	M	L	M	L
C2	M	H	M	H	M	M	M	H	M	M	M	M	M	M	L
R8C1	L	—	L	H	—	M	M	M	L	M	H	H	L	M	L
Total no. of L	8	2	5	11	10	2	2	2	6	8	14	13	10	9	6
Total no. of M	24	29	18	17	16	20	19	28	14	20	19	12	15	19	15
Total no. of H	4	4	5	8	9	6	15	6	8	8	3	3	11	8	7

holding between the different kinds of plant measurements for the same total concentration and also the relation holding between the same kind of plant measurements for different total concentrations and for different sets of salt proportions.

Table XII presents a correlation summary of all the quantitative plant data and shows the distribution of the high, medium, and low values obtained for each single criterion (yield, transpiration, and water requirement) as compared with those for the other criteria, the data being derived from those of table XI. The table as a whole is divided into an upper, middle and lower section, each of these sections referring to one of the three total concentrations here studied. It is divided vertically into four sections. The first of these presents the comparison between the yields of tops, on the one hand, and yields of roots, transpiration, and water requirements on the other. The second section gives the comparison between the root yields, on the one hand, and transpiration and water requirements on the other. The third section gives the comparison between transpiration, on the one hand, and the water requirement of tops and that of roots, on the other. The fourth and last section gives the comparison between the water requirement for tops and that for roots. The letters H, M and L, stand for high, medium, and low, as these terms have been used in table XI and in the preceding discussion.

The meaning of the numerical data of table XII is best brought out by examples. For the sub-optimal concentration, out of a total of four cultures giving high yields of tops, one gave medium, and three gave low yields of roots, all four gave high transpiration values and high water requirement for roots, and one gave medium and three low water requirement for tops. Similarly, of 24 cultures giving medium yields of tops, two gave high, 14 gave medium, and eight gave low yields of roots. All of the comparisons are stated in this manner. It will be seen that table XII may also be read in the vertical direction thus stating the comparison in the reverse order. For example, out of eight cultures with sub-optimal total concentration giving high root yields, two gave medium, and six gave low top yields. In order to bring out the dominant agreements and disagreements encountered in these comparisons the individual numerical data are marked in four different ways. Those numbers are printed in *italics* which represent more than half of the total number of cultures belonging in the group indicated by the letter (H, M, L) on the same line and at the *left* of that vertical section of the table. Thus, for the sub-optimal total concentration, the three cultures giving low root yields comprise more that one-half of the four cultures giving high top yields, and so this figure 3 appears in italics. Similarly, the 14 cultures giving medium root yields comprise more than half of the 24 giving medium top yields and the figure 14 is italicized. Reading the comparisons vertically, all those numbers that represent more than half of the total number of cultures belonging to the group indicated by the letter at the

TABLE XII

Relative distribution of high, low and medium dry weights, transpiration, and water-requirements for each of the three total concentrations here used, being a summary of the average data given in tables III, IV, V, IX, X and XI.

TOTAL CONCENTRATION	COMPARISON OF TOP YIELDS WITH ROOT YIELDS, TRANSPIRATION, AND WATER REQUIREMENT OF TOPS AND ROOTS										COMPARISON OF ROOT YIELDS WITH TRANSPIRATION AND WATER REQUIREMENT OF TOPS AND ROOTS									COMPARISON OF TRANSPIRATION WITH WATER REQUIREMENT OF TOPS AND ROOTS						COMPARISON OF WATER REQUIREMENT OF TOPS AND ROOTS			
	Yield tops	Yield roots			Transpiration			Water-requirement						Yield roots	Transpiration			Water-requirement						Transpiration	Water-requirement					Water req. tops	Water req. roots		
								Tops			Roots							Tops			Roots				Tops			Roots					
		H	M	L	H	M	L	H	M	L	H	M	L		H	M	L	H	M	L	H	M	L		H	M	L	H	M	L		H	M	L
Sub-optimal 0.10 atm.	H	—	1	3	4	—	—	—	1	3	4	—	—	H	—	8	—	3	5	—	—	1	**7**	H	4	8	3	**9**	6	—	H	3	2	3
	M	2	**14**	8	11	**13**	—	6	**14**	4	7	**15**	2	M	7	8	2	2	10	5	2	**12**	3	M	4	**11**	4	2	9	8	M	5	10	15
	L	**6**	2	—	—	6	2	2	5	1	—	—	8	L	8	3	—	3	5	3	9	2	—	L	—	1	1	—	—	2	L	3	3	2
Optimal 1.75 atm.	H	2	2	—	**4**	—	—	—	2	2	—	4	—	H	3	6	—	1	5	3	—	5	4	H	—	4	2	1	5	—	H	—	3	—
	M	7	12	10	2	**26**	1	2	**15**	12	8	15	7	M	2	12	2	1	9	6	—	**11**	5	M	3	14	11	7	14	7	M	4	9	6
	L	—	2	—	—	1	1	—	2	—	—	—	2	L	1	9	—	—	5	5	8	2	—	L	—	1	1	—	—	2	L	4	7	3
Supra-optimal 4.00 atm.	H	1	4	—	4	1	—	—	1	5	3	2	—	H	2	3	1	1	3	2	—	3	3	H	1	3	4	3	5	—	H	—	1	2
	M	4	**13**	1	4	**13**	1	1	**10**	7	4	**11**	3	M	6	10	4	2	9	9	6	**11**	3	M	—	7	7	4	7	3	M	1	7	4
	L	1	3	1	—	—	**5**	2	2	1	—	2	3	L	—	1	1	—	—	2	1	1	—	L	2	2	2	—	3	3	L	6	7	—

head of the column in which they occur are shown in black face type. Thus, for example, the six cultures giving low top yields comprise more than half of the eight giving high root yields, so that the figure 6 is in black type, but this same figure becomes also italicized because six is more than half of the eight cultures giving low root yields. Similarly, the figure 14 mentioned above as italicized is also in black face type, because 14 is more than half of the 17 cultures giving medium root yields. By this notation it is clear that the best correlations are indicated by black italics, where the agreement is good in both directions. Good agreement in the horizontal direction of comparison is indicated by italics and good agreement in the vertical direction is indicated by black type, which may be either italic or roman. Many of the points thus brought out have already been mentioned in the preceding discussions and space need not be here devoted to further consideration of these interesting agreements and disagreements.

Relation between the actual values for the various plant measurements

Finally, figure 15 is here presented to bring out the relations that hold between the actual values of the various plant measurements, which are represented graphically in much the same manner as that employed for figures 5, 9, 12, 13, and 14. In this case, however, the various different salt proportions (indicated at the base by the usual solution numbers) are all arranged in the decreasing order of their magnitudes for top yields of the optimal series. As in the previous graphs, a narrow line represents the optimal total concentration, a broad line represents the supra-optimal, and a narrow broken line represents the sub-optimal concentration. It will be seen that the figure shows five groups, each one of which comprises three graphs. The lower group (A, yield of roots) and the second group (B, yield of tops) are all plotted on the same scale and are directly comparable, as is indicated by the numbers at the left. The graphs of the third group (C, transpiration) are plotted on a different scale, which is indicated on the left margin. The fourth and fifth groups (D, water requirement per gram of tops, and E, water requirement per gram of roots) are all plotted on the same scale but the group E as a whole has been displaced downward in order to save space, as is clear from the ordinate values given at the left.

Inspection of figure 15 will bring out many of the relations between the various plant measurements, on the one hand, and the salt proportions and total concentration of the solution on the other, also between the different plant measurements for the same total concentration, the same set of proportions, etc. These graphs again emphasize the points already brought out, that the total concentration of the medium clearly determines the yield of tops (group B) and also the water requirement of tops (group D), for all salt proportions here tested; the order of magnitude with reference to total concentration is the same for all salt proportions in the case of either one of these

FIG. 15. Graphic summary of plant measurements.

two plant measurements, but the order for yield of tops is not at all the same as for water requirement of tops. The water requirement of tops is less as the total concentration of the medium increases, as has been found by other writers. The yield of tops, on the other hand, is greatest for the optimal, less for the supra-optimal, and least for the sub-optimal total concentration. Also, for transpiration (group C), the supra-optimal total concentration appears always to give the lowest value, for all the different sets of salt proportions, and the same generalization is true for nearly all the sets of salt proportions in the case of the water-requirement of roots (group E).

For yield of roots (group A) there is no general relation between the dry weights and the total concentration of the medium, but each particular set of salt proportions seems to have its own relations in this regard. Thus, solution R3C3 gives the highest root yield with the optimal total concentration, a medium yield with the sub-optimal, and the lowest with the supra-optimal. The same is true of solutions R5C2, R4C5, R1C4 and R2C2, but this is not true for any of the other sets of salt proportions. A similar shifting of the order of magnitude of the plant measurements, as related to the sub-optimal and optimal total concentrations, for different sets of salt proportions, is seen in the case of transpiration (group C) and water requirement of roots (group E), as has already been mentioned.

On the whole, the graphical summary of figure 15 shows clearly enough that the effect of any set of salt proportions is not, in general, relatively the same for different total concentrations, at least with the exception of the water requirement of tops, where there is considerable parallelism between the graphs for the optimal and supra-optimal series. It also shows that the effect of any total concentration is not generally the same for different sets of salt proportions. This summary shows, further, that root characters and top characters, of wheat grown as in these experiments, do not generally vary in the same way with reference to the conditions of the medium. Finally, it shows that different criteria for plant measurement may generally be expected to exhibit more or less pronounced differences in the relations between growth and the properties of the solution in which the plants are grown. Some of the details and exceptions to these generalizations are best brought out by study of the triangular diagrams previously given.

COMPARISON OF DRY WEIGHT YIELDS OF TOPS GROWN IN THE BEST SALT PROPORTIONS OF THE THREE-SALT SOLUTION, WITH THE CORRESPONDING YIELDS FROM SOLUTIONS EMPLOYED BY OTHER AUTHORS

As previously stated, Knop's solution and Tottingham's best solution for tops (T3R1C4) were included in each of the three experimental series here carried out, for purposes of comparison.

For the sub-optimal series (0.1 atm.) the highest average yield of tops (culture R4C5) was 1.65 times the top yield obtained from culture R1C1. The average yields of tops obtained from Knop's solution and from Tottingham's best solution, both having the same total concentration as culture R1C1 (0.1 atm.), were 1.35 and 1.62, respectively. Thus the three-salt solution with proportions giving the highest yield of wheat tops, shows an improvement of 22 per cent over Knop's solution, while Tottingham's best solution shows an improvement over Knop's solution of 20 per cent, all for a total concentration of 0.1 atmosphere.

For the optimal series the highest average yield of tops (culture R5C2) was 1.39 relative to the yield from culture R1C1. The corresponding yields obtained from Knop's solution and from Tottingham's best solution for tops were 1.09 and 1.27, respectively, relative to the same control. For this total concentration (1.75 atm.) the best salt proportions of the three-salt solution produced an average dry weight of wheat tops 28 per cent higher than the yield obtained from Knop's solution with the same total concentration, while Tottingham's best solution for wheat tops produced a corresponding average yield 17 per cent above that obtained from Knop's solution.

For the supra-optimal series (4.0 atm.), the highest average dry weight of tops (culture R4C3) was 1.38 relative to the yield obtained from culture R1C1. Knop's solution and Tottingham's best solution for tops, with the same total concentration, yielded corresponding dry weights of 1.05 and 1.23, respectively. The best salt proportions of the 3-salt solution with this total concentration (4.0 atm.) showed an improvement of 31 per cent over Knop's solution, while Tottingham's best solution showed a corresponding improvement of 17 per cent.

In order to compare 3-salt solution R5C2, which produced the highest yield of wheat tops in the optimal series of the present studies, with Tottingham's best solution for wheat tops and with Knop's solution, all *with the same total concentration as was employed by Tottingham* (2.50 atm.) a series of three cultures of each of these three solutions, all having a total concentration of 2.50 atmospheres, was carried out during the 23-day period from February 25 to March 19, 1915. The average dry weight of tops produced by three-salt solution R5C2, relative to the average yield produced by Knop's solution was 1.22, and the corresponding average yield from Totting-

ham's best solution for tops was 1.07. Therefore, with a total concentration of 2.50 atmospheres, Tottingham's best solution produced a yield of tops 7 per cent higher than that obtained from Knop's solution, while the three-salt solution with the best salt proportions for wheat tops produced a corresponding yield 22 per cent higher than that produced by Knop's medium. The data for all these comparisons are presented in table XIII, which gives the volume-molecular partial concentrations of the solutions and the average dry weights of tops, relative to the yields obtained from the same total concentration of Knop's solution taken as unity. The actual values obtained with Knop's solution are given in parenthesis below the assumed relative values of unity.

TABLE XIII

Comparison of yields of wheat tops obtained from various total concentrations of Knop's solution, Tottingham's solution No. T3R1C4, and 3-salt solution No. R5C2.

TOTAL CONCENTRATION	NAME OF SOLUTION	PARTIAL MOLECULAR CONCENTRATIONS				YIELD OF TOPS RELATIVE TO THAT FROM KNOP'S SOLUTION
		KNO_3	KH_2PO_4	$Ca(NO_3)_2$	$MgSO_4$	
atm.		*g.-mol. per l.*	*g.-mol. per l.*	*g.-mol. per l.*	*g.-mol. per l.*	
0.10	Knop's solution	0.00028	0.00022	0.00070	0.00024	1.00
	Tottingham's solution No. T3R1C4	0.00062	0.00019	0.00058	0.00046	1.20
	3-salt solution No. R5C2	.....	0.00082	0.00074	0.00028	1.22
						(0.3527)
1.75	Knop's solution	0.0059	0.0044	0.0145	0.0050	1.00
	Tottingham's solution No. T3R1C4	0.0034	0.0108	0.0101	0.0081	1.17
	3-salt solution No. R5C2	.....	0.0180	0.0052	0.0150	1.28
						(0.4485)
2.50	Knop's solution	0.0083	0.0063	0.0210	0.0070	1.00
	Tottingham's solution No. T3R1C4	0.0049	0.0156	0.0144	0.0116	1.07
	3-salt solution No. R5C2	.....	0.0257	0.0074	0.0214	1.22
						(0.6807)
4.00	Knop's solution	0.0198	0.0147	0.0488	0.0166	1.00
	Tottingham's solution No. T3R1C4	0.0114	0.0354	0.0336	0.0278	1.17
	3-salt solution No. R5C2	.....	0.0368	0.0198	0.0428	1.31
						(0.3774)

The comparative efficiencies of the 3-salt solutions R5C2 and R3C3 of the optimal series, with the best and second best salt proportions for dry weight yields of wheat tops, respectively, and of various other nutrient solutions commonly employed by workers in physiology, were determined by a special experiment. This experiment consisted in a duplicate series of cultures, all having a total concentration of 1.75 atmospheres, which was conducted during the 24-day period from December 17, 1914, to January 10, 1915.

The following eleven solutions devised by earlier writers were included

in this comparison. The formulas are given in the list below, in terms of gram-molecules per liter (m). A trace of ferric phosphate was added to the solutions for which iron is not mentioned in the formula. As thus made up these solutions all agree with the two 3-salt solutions with which they are compared in having a total concentration of 1.75 atmospheres.

Birner and Lucanus'[31] *solution:* $Ca(NO_3)_2$, 0.0133 m; KH_2PO_4, 0.0108 m; $MgSO_4$, 0.0061 m; $Fe_3(PO_4)_2$, 0.0043 m.

Crone's[32] *solution:* KNO_3, 0.0266 m; $Ca_3(PO_4)_2$, 0.0022 m; $Fe_3(PO_4)_2$, 0.0019 m; $MgSO_4$, 0.0056 m; $CaSO_4$, 0.0049 m.

Detmer's[33] *solution:* $Ca(NO_3)_2$, 0.0149 m; KH_2PO_4, 0.0035 m; $MgSO_4$, 0.0051 m; KCl, 0.0083 m.

Hartwell,[34] *Wheeler and Pember's solution:* $Ca(NO_3)_2$, 0.0136 m; $CaH_4(PO_4)_2$, 0.0027 m; $MgSO_4$, 0.0077 m; KCl, 0.0075 m.

Knop's [1862] *solution:* KNO_3, 0.0059 m; KH_2PO_4, 0.0044 m; $Ca(NO_3)_2$, 0.0145 m; $MgSO_4$, 0.0050 m.

Pfeffer's[35] *solution:* $Ca(NO_3)_2$, 0.0136 m; KNO_3, 0.0056 m; KH_2PO_4, 0.0041 m; $MgSO_4$, 0.0046 m; KCl, 0.0037 m.

Sachs' [1860] *solution:* KNO_3, 0.0155 m; $Ca_3(PO_4)_2$, 0.0025 m; $MgSO_4$, 0.0065 m; $CaSO_4$, 0.0075 m; NaCl, 0.0067 m.

Schimper's[36] *solution:* $Ca(NO_3)_2$, 0.0118 m; KNO_3, 0.0048 m; KH_2PO_4, 0.0028 m; $MgSO_4$, 0.0040 m; NaCl, 0.0083 m.

Schreiner and Skinner's solution: $NaNO_3$, 0.0278 m; $CaH_4(PO_4)_2$, 0.00066 m; K_2SO_4, 0.0030 m.

Tollens'[37] *solution:* $Ca(NO_3)_2$, 0.0128 m; KNO_3, 0.0052 m; KH_2PO_4, 0.0038 m; $MgSO_4$, 0.0049 m; NaCl, 0.0054 m.

Tottingham's [1914] *solution:* KNO_3, 0.0034 m; KH_2PO_4, 0.0108 m; $Ca(NO_3)_2$, 0.0101 m; $MgSO_4$, 0.0081 m.

Table XIV presents the results of this comparative study. The notation of this table is self-explanatory. The solutions are arranged in the order of the total dry weight produced.

From table XIV it is clear that the two 3-salt solutions here tested (R5C2

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[31] Birner, H., and Lucanus, B., Wasserkulturversuche mit Hafer in der Agric.-Chem. Versuchsstation zu Regenwalde. Landw. Versuchsst. **8:** 128–177. 1866. Note that this solution contains the same main salts as do the 3-salt solutions that are the subject of the present study, and that its proportions are nearly the same as those of 3-salt solution R3C6. The iron of Birner and Lucanus' solution is supplied as *ferrous* phosphate, however.

[32] Crone, G., Ergebnisse von Untersuchungen über die Wirkung der Phosphorsäure auf die höhere Pflanzen und eine neue Nährlösung. Sitzungsber Neiderrhein. Ges. Nat.-und Heilk. Bonn. 1902. Pages 167–173.

[33] Detmer, W., Practical plant physiology, translated by S. A. Moor. London, 1898. Page 2.

[34] Hartwell, B. L., Wheeler, H. J., and Pember, F. R., The effect of the addition of sodium to deficient amounts of potassium upon the growth of plants in both water and sand cultures. Ann. Rep. Rhode Island Agric. Exp. Sta. **20:** 299–357. 1907.

[35] Pfeffer, W., The physiology of plants, translated by A. J. Ewart, **1:** 420. Oxford, 1900.

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[37] Tollens, B., Ueber einige Erleichterungen bei der Cultur von Pflanzen in wässerigen Lösungen. Jour. Landw. **30:** 537–540. 1882.

and R3C3, total concentration 1.75 atm.) proved to be as good as or better than any of the other solutions mentioned, when employed with this total concentration. These two 3-salt solutions may be considered as practically equal in the production of top yields and of total dry weight, but it appears from the data just given that solution R5C2 is considerably better suited to the production of root yields than is solution R3C3. This latter indication is not clearly borne out by the other tests of these solutions, however. From table IV it is seen that solution R3C3 (1.75 atm.) gave in one instance (series A) a somewhat higher yield of roots than did solution R5C2 in the same test. On the other hand, in another test (series B) the relation between

TABLE XIV

Relative dry weights of tops and of roots of wheat grown 24 days (Dec. 17, 1914, to Jan. 10, 1915) in various nutrient solutions, all having a total osmotic concentration of 1.75 atmospheres.

AUTHOR OF SOLUTION	RELATIVE YIELD OF TOPS	RELATIVE YIELD OF ROOTS	RELATIVE TOTAL DRY WEIGHT
Sachs	1.00*	1.00	1.00
	(0.362)	(0.134)	(0.497)
Schimper	0.95	1.14	1.00
Detmer	0.95	1.22	1.03
Tollens	1.28	1.10	1.23
Schreiner and Skinner	1.42	0.83	1.26
Hartwell, Wheeler and Pember	1.55	0.96	1.39
Pfeffer	1.52	1.13	1.41
Knop	1.60	1.07	1.45
Tottingham	1.77	1.13	1.60
Crone	1.95	1.05	1.70
Birner and Lucanus	1.93	1.17	1.72
Shive, R3C3	1.93	1.16	1.73
Shive, R5C2	1.93	1.22	1.74

* The data are each expressed in terms of the corresponding value obtained from Sachs' solution, considered as unity. The actual values for Sachs' solution in grams, are given in parenthesis.

these two solutions, as to root yield, is reversed, and is similar to that brought out in table XIV. The averages of series A and B (table IV) indicate that these two solutions are practically equal in the production of root yields. These same averages indicate that solution R5C2 gives top yields a little higher than those obtained from solution R3C3. On the whole, it seems advisable to employ solution R5C2 (1.75 atm.) as the best solution, for wheat, resulting from the present study.

The only instance in which a yield of 3-salt solution R5C2 (1.75 atm.) is surpassed by one of the other solutions with 1.75 atmospheres of total concentration occurs with Crone's solution, which gave a slightly higher yield of tops than did solution R5C2 (1.95 as compared to 1.93). But

Crone's solution here gave a much lower yield of roots and a slightly lower total yield than did solution R5C2.

Two instances are recorded in table XIV showing other solutions as giving yields equal to the corresponding one from solution R5C2. (1) Birner and Lucanus' solution gave as high a top yield, but it fell far below solution R5C2 in root yield and slightly below it in total yield. Solution R3C6 of the present study, which has the same main salts in nearly the same proportions as has Birner and Lucanus' solution, appears to be markedly inferior to solution R5C2 in the production of both tops and roots, according to the data of table IV (page 349). But the Birner and Lucanus solution contains ferrous phosphate ($Fe_3(PO_4)_2$) instead of the ferric salt employed with the 3-salt solutions of the present paper. (2) Detmer's solution equals solution R5C2 in root yield but is obviously very poor by the criterion of top yield and by that of total dry weight.

It should be emphasized in this connection that the conclusions here reached, as to the relative values of these various solutions, are to be taken as established only for the total concentration here employed (1.75 atm.), and for the kind of plant here used (winter wheat), during the first four weeks of its development from the seed. Whether some of the other solutions listed in table XIV may or may not surpass 3-salt solution R5C2, when used with other total concentrations, or with other plants, or other developmental stages of the same plant, or even under other climatic conditions cannot now be stated.

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